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Created in 1849 the Department of the Interior—a department of conservation—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

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ANNUAL MARKS ON SHELL AND LIGAMENT OF SEA SCALLOP (*PLACOPECTEN MAGELLANICUS*)

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ABSTRACT

The annual rings on the shell of the sea scallop are frequently weak or obscured by other rings caused by some nonannual stress. Methods are presented by which it is possible to locate the true annual rings by reference to marks on the resilium, changes in shell curvature, changes in color pattern, weight of the shell, and areas of attack by boring organisms. The results obtained are validated by comparing a growth rate derived through location of the annual rings with one derived from the growth increments of a large sample which had been tagged and released and recaptured after a year at large. The objectivity of the criteria used to identify the annual rings was tested.

ANNUAL MARKS

Many investigators have been able to determine the growth rate of various species of mollusks by identifying those rings on the shell that are caused by some consistent annual phenomenon. Measuring the amount of shell between the rings provides data from which it is possible to estimate growth rates for various areas and year classes. Canadian investigators (Stevenson and Dickie, 1954; Dickie, 1955) succeeded in applying this technique to the sea scallop, *Placopecten magellanicus* (Gmelin), of the Bay of Fundy. Dickie (personal communication) also succeeded, with some difficulty, in locating annual rings on the sea scallops of Georges Bank. His difficulty was caused by the fact that the annual rings are usually rather weak and frequently masked by the presence of strong shock rings. Sea scallops are rather sensitive creatures, and any serious disturbance causes them to mark the event with a shock ring on the shell (Posgay, 1950). The grounds that interest us most are those on Georges Bank, which sustain the heaviest fishing pressure and where concentrated dredging operations may cause uncaught scallops to form many shock rings (fig. 1).

Because of the difficulties of interpreting the rings on the shell, we have examined some of the other hard parts of the sea scallop for characteristics that might offer clues to age. The most useful of these structures proved to be the calcareous part of the resilium. Areas attacked by boring organisms, weight of the shell, color changes, and changes in the curvature of the shell also provided valuable clues to age.

This paper describes the methods used to determine the position of the annual rings, gives the result of applying them to a sample of shells, compares the derived growth rate with the growth rate determined from tagged and recaptured animals, and gives the result of an experiment testing the objectivity of the criteria. Each phase of the work was carried out by a different investigator to avoid subjective bias.

RINGS ON THE SHELL

The surface of the shell of the sea scallop is covered with a series of fine concentric lines (circuli) as a result of the addition of new shell along the margin during growth. At intervals,

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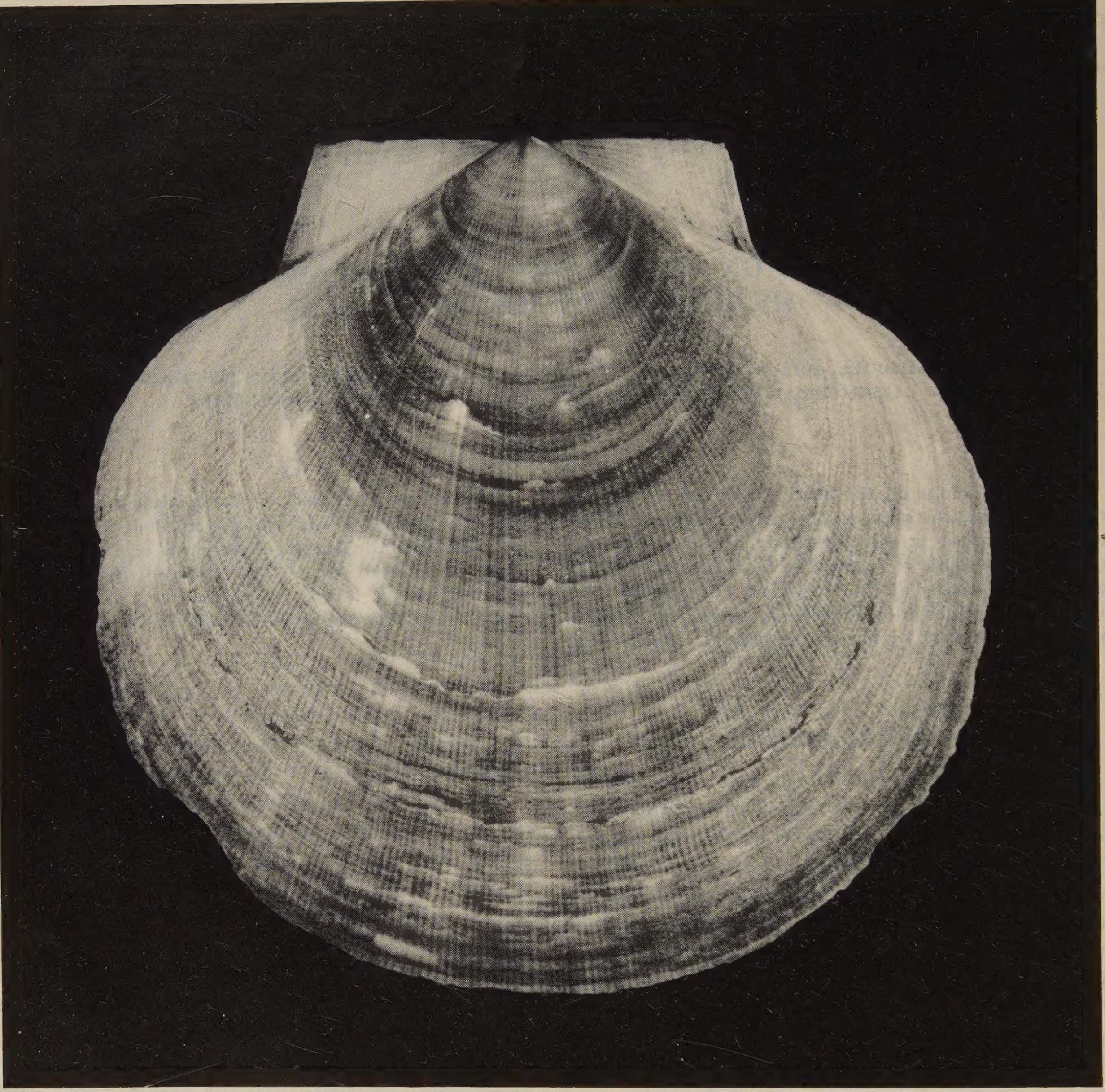

FIGURE 1.—Upper valve of sea scallop showing strong shock rings and weak annual rings.

the circuli are more closely spaced and give the appearance of a band or ring (fig. 2). These bands are laid down annually as the result of a decrease in the rate of growth much as has been demonstrated for tree rings and fish scales. Although the cause has not yet been demonstrated, we believe that it is low winter temperatures. Specimens from shallow water (fig. 3), where winters are more severe, have more prominent rings than those from deeper water where temperatures vary less. Georges Bank, with an average annual temperature range of 8°–12° C., has a particularly equable climate for sea scallops. Posgay (1953) has shown that sea scallops grow fastest at about 10° C. In his experiments, the rate dropped to about 95 percent of the maximum at 8° C. and to about 80 percent at 12° C.

In addition to the annual rings, most sea scallop shells exhibit other annuli which mark nonannual

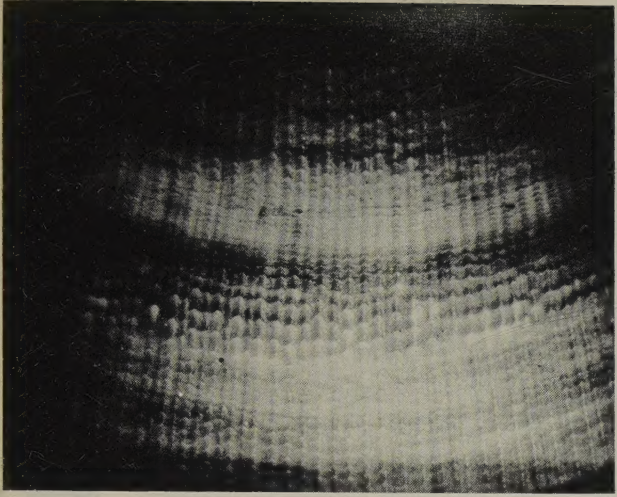

FIGURE 2.—Closeup view of a portion of the upper valve of a sea scallop, showing a band of narrowly spaced circuli between two areas of widely spaced circuli.

phenomena. In shallow water, a severe storm may cause sufficient disturbance on the bottom to cause the scallops to form shock rings. Offshore, shock rings are usually caused by dredging activities of the fishing fleet. Lightly fished areas yield unmarked scallops, while heavily fished areas yield scallops whose shells are a confusion of shock rings. These injuries are sometimes so severe as to distort the shape of the shell (fig. 4).

On Georges Bank, which provides more than 75 percent of the sea scallop catch, both phenomena, weak annual rings and many shock rings, combine to make the location of the annual rings difficult (fig. 1). Not all scallops, however, react in the same degree to the stress that causes the annual ring. Any reasonably large sample will contain some sensitive individuals bearing clear annual rings. Likewise, not all scallops are subjected to disturbances sufficient to cause many shock rings. It is usually possible, therefore, to sort out at least a few shells which are fairly easy to interpret. While such a small sample of selected individuals cannot give a valid estimate of the growth rate of the population, it can give an idea of what to expect from the rest of the sample. The more deeply curved valve, which is uppermost when the scallop is at rest, usually bears the clearest annual rings; but in some individuals, the lower valve will be more easily interpreted.

MARKS ON THE LIGAMENT

The structure and the function of the ligament in *Pecten* have been fully described by Trueman (1953a, and 1953b). The outer layer (fig. 5) unites the two valves and acts as a flexible hinge. The inner layer, the resilium, is composed of a large, dark-brown, conical, central structure of rubbery, noncalcareous material and two small lateral calcareous plates, which cement the resilium into a shallow socket, the resilifer, on each valve. The resilium acts as a sort of compressible spring working in opposition to the adductor muscle. When the muscle is relaxed, the resilium forces the margins of the valves apart.

As the scallop grows and adds new shell along the margins, it also adds new material to the ligament. When shell growth slows or ceases, ligament growth also slows or ceases producing a mark. The resilium, and the epithelial cells which produce it are well protected and less exposed to shock and injury than are the margins of the shell and the cells which produce it. Therefore, marks on the resilium caused by an annual period of slow growth are relatively more prominent compared with shock marks than are the corresponding marks on the shell. The spaces between the bands on the resilium are proportional to the spaces between the bands on the shell; hence, a specific area of the resilium can be referred to a corresponding part of the shell. This section of the shell can then be studied closely in search of the annual ring.

Figure 6 shows the upper valve of a sea scallop, selected because of its distinct annual rings and lack of strong shock rings, which has been sawed down the midline. The numbers indicate annual rings. Figure 7 shows the resulting cross section of the hinge area of the same scallop. The dark area in the center of the cross section is the resilium; the lighter areas immediately to the left and right are the calcareous plates. The numbered, darker bands on the plates and the constrictions of the resilium correspond to the five annual rings on the shell.

It is not necessary to make a cross section in order to observe the annual marks on the plates of the resilium. When the valves of a sea scallop are separated, the resilium usually splits down the middle. After drying for a few days, the remaining half of the resilium, including the attached

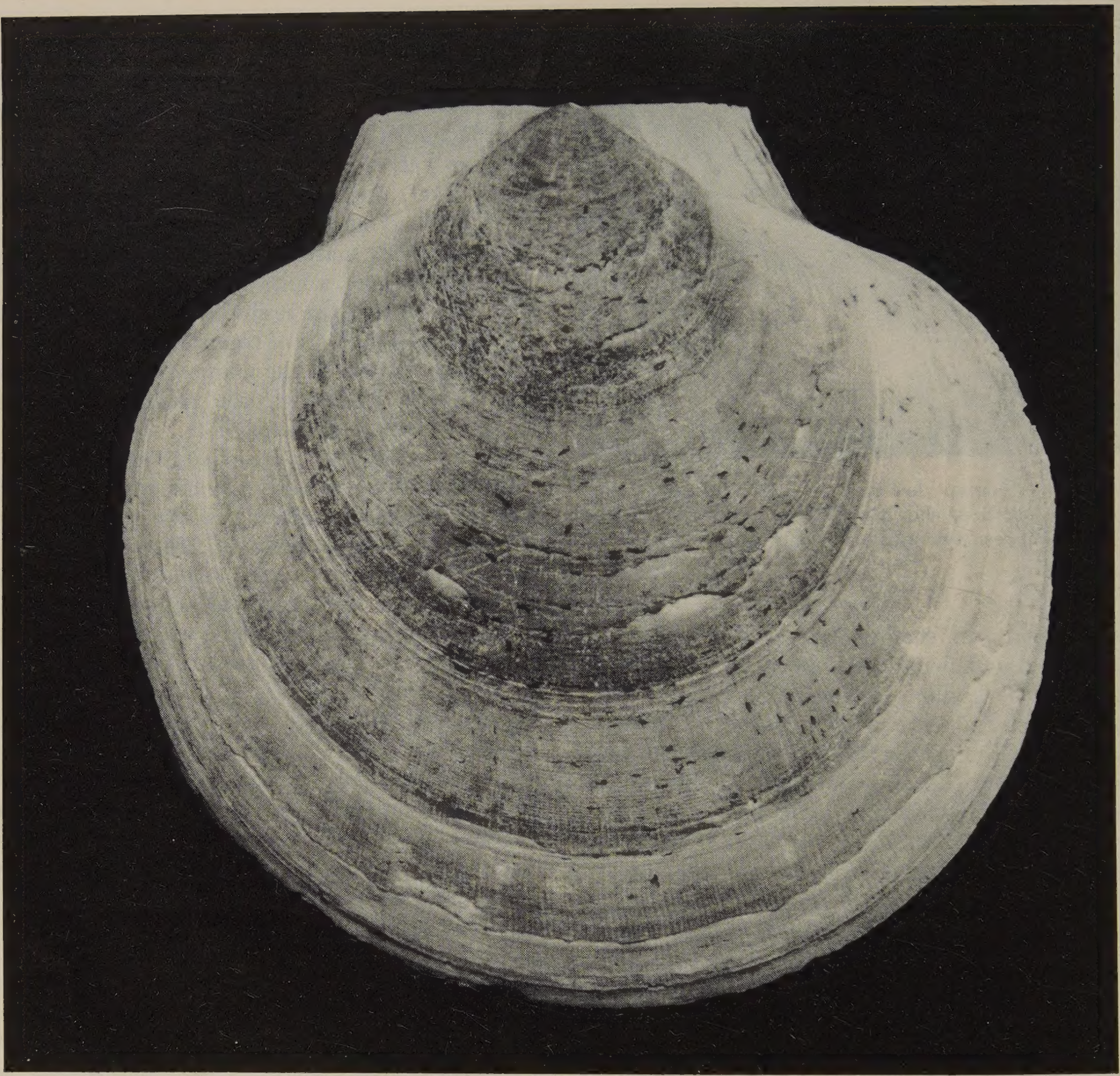

FIGURE 3.—Upper valve of a sea scallop taken from shallow water showing prominent annual rings.

calcareous plate, can be easily picked out of the resilifer. The plate can then be examined with a low-power microscope or hand lens (fig. 8). If the ligament has been lost, it is still possible to examine the corresponding impression on the resilifer.

OTHER SHELL CHARACTERISTICS

In some areas, annual invasions of boring organisms infect the upper valve of the sea scallop (figs. 6 and 9). The areas of heaviest infestation can be easily seen if the shell is held over a strong light. The annual rings can usually be located between the infected areas. The weight of the shell is sometimes an index of rate of growth. A thin shell is usually the sign of a fast growing individual; a thick, heavy shell usually means slow growth. Some shells exhibit areas of convex curvature between the annual rings (fig. 10). The profile of these shells, held at arm's length, show a series of hills and valleys. The annual rings can usually be found in the valleys. An occasional shell, or sample of shells from particular areas, will show changes in color pattern of an annual

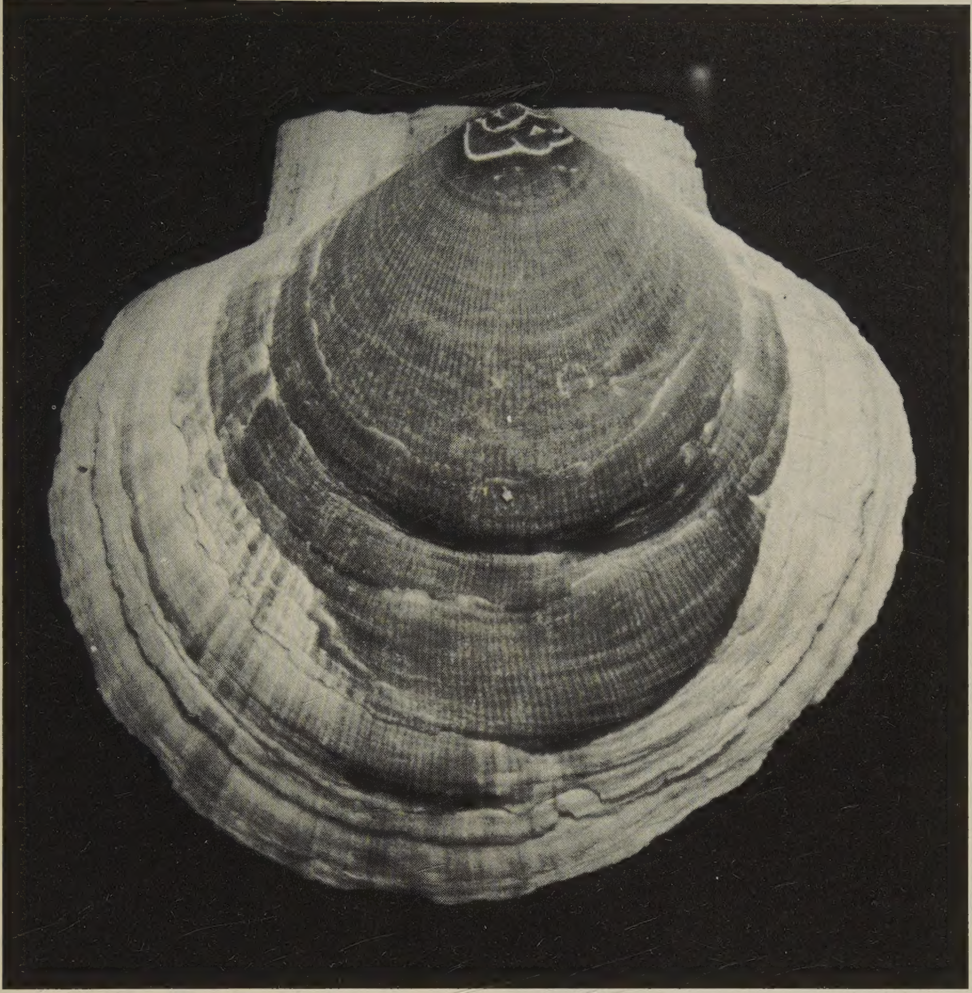

FIGURE 4.—Upper valve of a sea scallop taken from a heavily fished area, showing malformation as a result of injury to the mantle.

nature which may help to locate the rings (fig. 11). Figures 9, 10, and 11 represent selected individuals; obviously, not all shells are so strikingly marked.

READING A SAMPLE

The shells to be read must first be cleaned of all foreign matter. It is best to soak them in a strong solution of a nonbleaching detergent and then scrub them with a wire brush. The length frequency is determined to see if the sample is polymodal. We define length for these purposes as being measured along the greatest diameter of the shell from umbo to opposite margin. Shells that do not have a large number of shock rings and appear to have prominent annual rings are then sorted out. The shells and resilia of these individuals are studied first, and a preliminary table of length at time of annual ring formation is prepared.

With this table as a guide to the most probable location of the annual rings the rest of the sample is read. It is best to work from the smaller to the larger specimens. All of the clues mentioned previously are used as occasion demands and opportunity affords. The more difficult shells are set aside until the last when the averages and the deviations are more firmly established. These, as well as the larger, older shells with the annual rings near the margin crowded together, can usually be best interpreted by reference to the resilia.

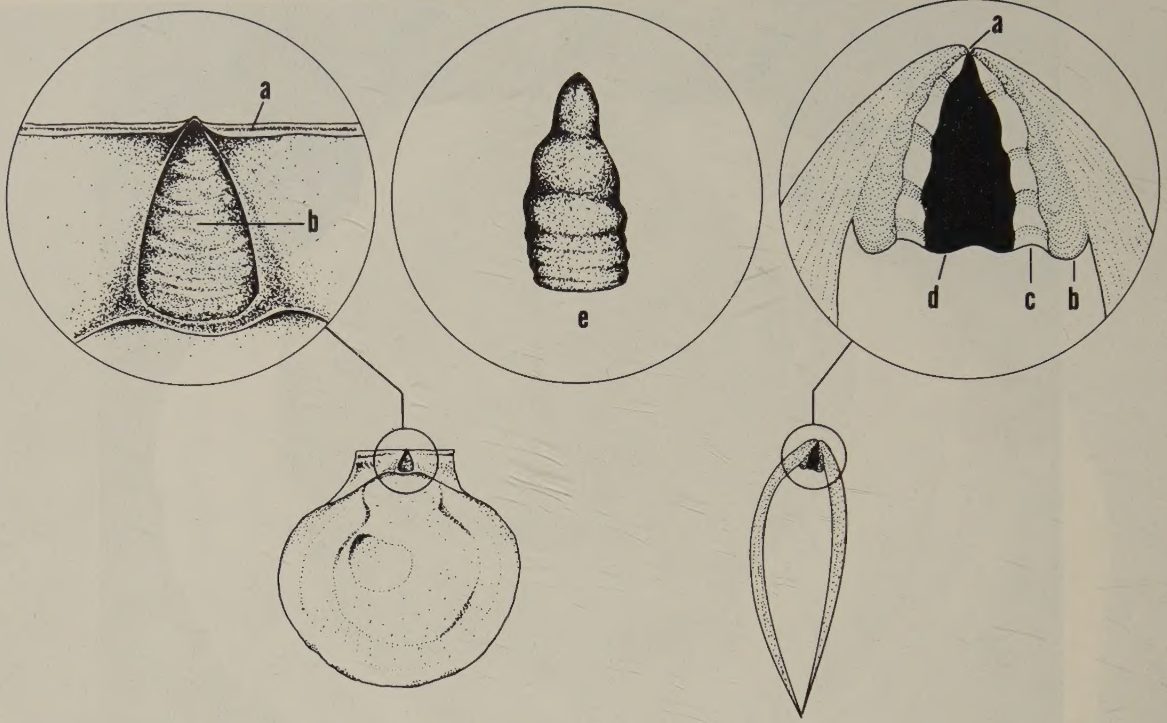

FIGURE 5.—Hinge and ligament of the sea scallop. (a) Outer layer of the ligament at hinge line, (b) resilifer, (c) calcareous plates of the resilium, (d) compressible part of the resilium, and (e) surface view of calcareous plate.

VALIDATION OF THE METHOD

In September of 1957, we had tagged and released 5,375 sea scallops on the northeast peak of Georges Bank. A fine hole is drilled in the ear of the upper valve just over the byssal notch in the lower valve. A stainless steel pin, bearing a numbered Petersen disc and a 6-inch yellow plastic streamer, is pushed through the hole and bent over to hold the tag securely (fig. 12). The animal is not wounded but the disturbance of dredging, handling, and tagging is sufficient to put a strong shock ring on the shell. The margin is nicked with a triangular file so that this tagging shock ring can be identified with certainty later. After recapture it is simple to measure how much new shell has been added since the date of tagging and, with a large enough sample, calculate the growth rate.

This particular tagging experiment had been very successful and we had a great many shells from recaptured animals. One group of 411 had been recaptured only a few weeks after release and therefore had added very little new shell. With the techniques described previously, the annual rings on this group were located and the shell lengths at the time of formation of each ring measured (table 1). The Walford (1946) regression equation calculated from the average length at the time of ring formation is: $L_{t+1}=42.4+0.706 L_t$ (equation 1).

We also had 392 shells from animals that had been captured, tagged, and released at the same

TABLE 1.—*Average length (mm.) at time of ring formation for 8 year classes in sample of 411 sea scallops and average for all year classes combined*

Ring No.	Year class								Average
1	22.0	20.4	21.3	20.6	23.5	21.1	18.9	24.7	20.7
2	54.1	52.7	52.1	50.7	55.5	50.6	52.7	56.3	52.6
3	84.4	80.8	80.5	78.6	79.6	78.2	80.3	83.3	80.7
4	------	100.9	100.3	97.4	97.9	97.8	97.9	99.1	98.7
5	------	------	112.4	110.7	110.5	109.4	110.5	110.3	110.6
6	------	------	------	120.4	119.9	119.3	119.6	119.2	119.7
7	------	------	------	------	126.4	126.9	127.4	126.3	126.7
8	------	------	------	------	------	132.2	132.3	131.8	132.1
9	------	------	------	------	------	------	136.1	136.2	136.1
10	------	------	------	------	------	------	------	139.2	139.2
Number in year class	36	74	98	88	50	36	17	14	------

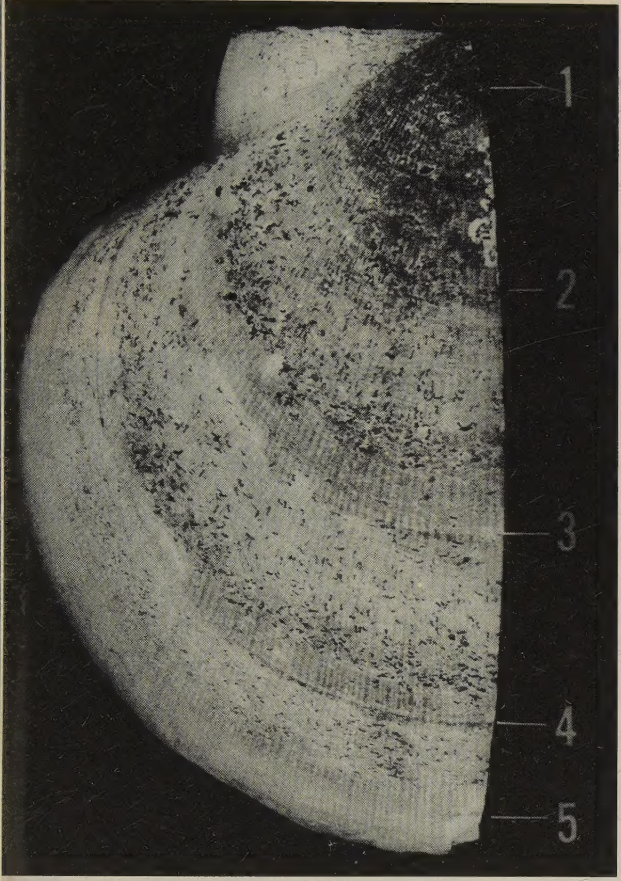

FIGURE 6.—Sea scallop shell with five prominent annual rings. The shell between the rings shows annual attacks by boring organisms.

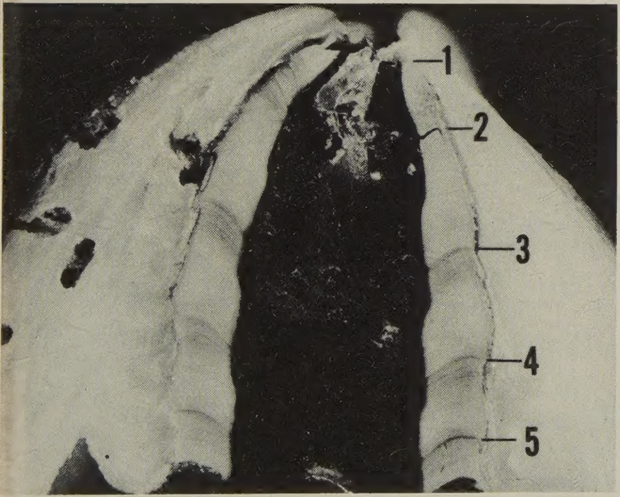

FIGURE 7.—Cross section of hinge of sea scallop showing annual marks in the calcareous plates of the resilium.

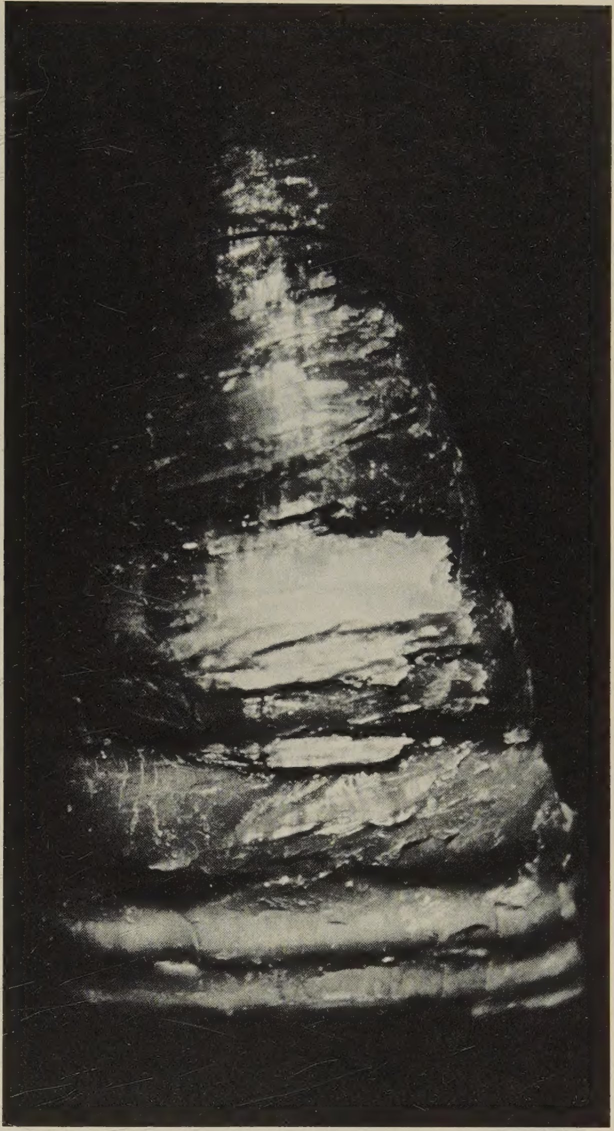

FIGURE 8.—Calcareous plate of a resilium showing banding and constriction in response to some annual stress.

time and location but which had been at large from 48 to 68 weeks before being recaptured. These shells were grouped by 2-week intervals, and the length when tagged (L_0) and the length when recaptured (L_r) measured on each one (table 2). The Walford (1946) regression of length at recapture on length when tagged was then calculated for each of the five groups. The tabulation below shows the number in each sample, the time at large, and the slope and intercept of the regression equations.

Sample No.	N	Weeks out	Slope	Intercept
1	140	49.6	0.6384	50.30
2	89	58.1	.6430	50.53
3	46	60.7	.6601	48.16
4	62	64.1	.5897	57.20
5	55	66.7	.5879	57.42

These regression equations, each of which represented growth for a different time interval, were then transformed to a common, 52-week, time interval using Lindner's (1953) method.

Sample No.	Weeks out	Slope	Intercept
1	52	0.6248	52.21
2	52	.6735	46.21
3	52	.7005	42.43
4	52	.6516	48.57
5	52	.6608	47.26

Taking an average slope and intercept gives $L_{t+1}=47.3+0.662\ L_t$ (equation 2) as the estimate of growth per year by this method.

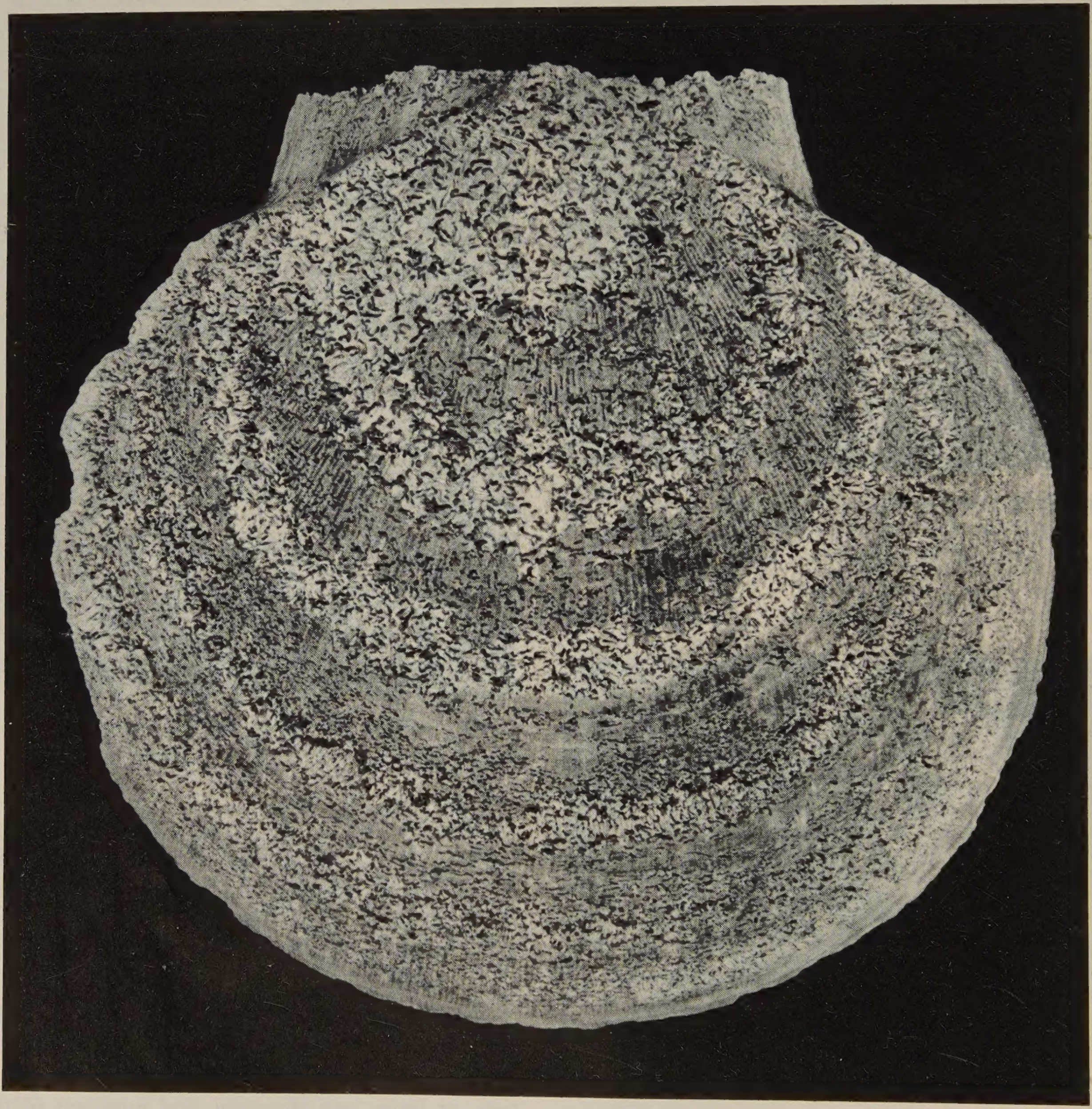

FIGURE 9.—Upper valve showing the result of heavy invasion of boring organisms. The annual rings are located between the areas of heaviest damage.

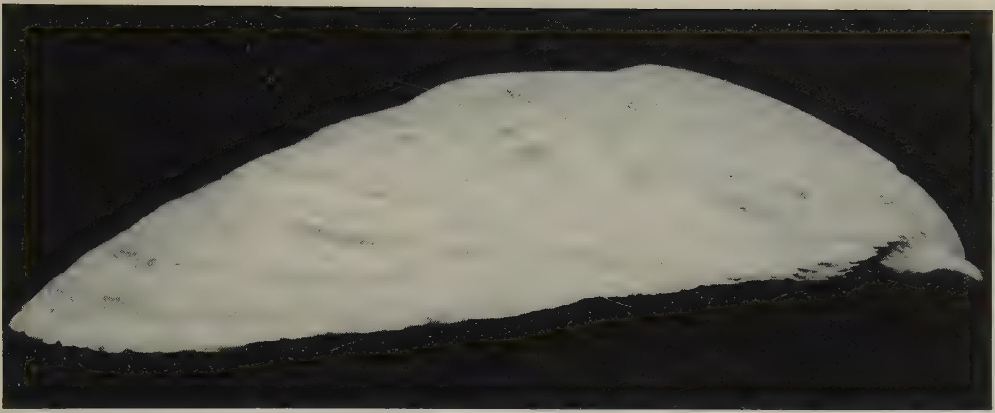

FIGURE 10.—Profile of the upper valve of a sea scallop. The annual rings are found in the areas of concave curvature.

TABLE 2.—*Length (mm.) of 392 sea scallops when tagged* (L_g) *and released at latitude 41°52′ N., longitude 66°23′ W., on Sept. 22, 1957, and when recaptured* (L_r) *about 1 year later*

SAMPLE 1, OUT 49.6 WEEKS

L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r
85.0	109.6	102.2	115.0	111.9	120.5	119.2	126.9	125.4	128.7
89.1	110.2	102.5	120.6	112.0	124.9	119.2	127.7	125.4	130.7
89.9	107.1	102.6	116.1	112.2	120.9	119.2	132.3	125.7	135.0
90.1	104.7	102.8	120.6	112.3	125.9	119.3	122.3	126.2	129.4
90.8	110.1	103.3	113.8	112.8	123.1	119.4	126.2	126.3	133.1
90.9	111.0	104.2	117.3	114.0	120.0	119.5	122.3	126.5	129.4
91.0	106.5	104.7	115.7	114.1	123.2	119.6	125.1	126.5	132.1
92.0	109.8	105.0	113.9	114.7	123.4	119.9	124.1	126.7	132.2
92.2	106.8	105.7	115.0	114.7	123.6	120.0	127.7	126.7	132.4
93.6	112.0	105.9	115.0	115.2	117.7	120.2	127.7	127.4	131.8
95.3	115.0	106.4	120.0	115.5	124.1	120.2	129.3	127.4	132.6
95.4	114.9	107.0	117.9	115.9	121.4	120.6	125.4	127.7	132.0
95.6	108.5	107.1	119.6	116.1	125.1	120.6	125.6	127.8	130.7
96.3	113.2	107.1	120.0	116.1	127.7	121.1	126.1	128.7	131.5
96.5	113.9	108.2	115.7	116.3	127.2	121.2	124.3	129.4	134.2
96.6	102.2	108.7	119.0	116.4	124.0	121.3	127.4	129.8	137.0
97.1	117.1	108.9	117.2	116.4	126.0	121.3	129.8	130.4	135.0
97.4	112.0	109.1	121.8	116.9	123.0	121.4	125.4	131.0	136.4
97.5	119.8	109.6	119.3	117.1	123.3	121.8	125.8	131.3	133.4
97.6	109.3	109.8	122.8	117.4	126.5	122.4	130.2	131.6	135.8
99.5	116.1	110.2	120.4	117.8	126.7	122.5	126.5	131.6	136.1
100.5	113.6	110.2	121.6	117.9	122.5	122.8	126.2	131.8	134.4
101.3	109.2	110.4	122.3	118.0	125.6	122.9	130.8	132.6	139.4
101.5	107.5	111.6	119.0	118.0	126.5	123.6	126.9	132.8	135.8
101.6	108.6	111.6	122.0	118.0	127.9	123.7	125.0	133.4	136.9
101.6	115.0	111.6	122.4	118.2	126.2	123.7	126.4	133.7	137.6
101.7	115.4	111.7	123.7	118.6	125.3	123.7	129.9	134.3	137.6
101.8	113.1	111.7	123.0	118.8	125.6	124.9	132.8	134.4	136.6

SAMPLE 2, OUT 58.1 WEEKS

L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r
85.6	106.0	100.7	120.0	111.8	120.4	119.2	125.0	127.1	134.7
86.9	107.3	101.7	115.8	112.4	120.5	119.7	129.1	127.2	133.5
87.9	105.1	101.8	111.6	112.6	126.2	120.0	129.3	128.5	136.4
88.8	113.9	103.0	116.6	113.3	120.4	120.6	129.9	129.7	133.4
90.3	115.3	103.5	115.2	113.5	119.4	121.0	126.0	130.7	137.6
90.9	103.0	104.5	115.2	113.9	123.8	121.3	126.0	130.9	135.0
90.9	108.3	104.9	115.6	114.4	120.6	121.4	128.5	131.0	134.5
90.9	114.4	105.0	117.2	115.0	125.6	121.9	127.0	131.0	135.3
91.8	105.7	106.2	117.4	115.4	123.9	122.8	134.1	132.9	135.4
91.9	112.3	106.3	118.5	115.6	125.4	122.9	127.9	133.7	136.7
94.7	107.5	107.1	121.8	115.9	127.1	124.0	133.8	133.8	138.3
95.0	115.3	107.2	118.9	115.9	127.5	124.6	129.7	133.9	136.4
95.3	113.3	109.1	116.9	116.1	124.0	124.9	128.1	134.0	137.3
98.6	110.4	109.4	118.7	116.2	125.6	125.0	128.9	134.4	140.6
98.6	116.1	110.7	118.5	117.4	123.3	126.0	133.4	134.6	136.1
99.4	114.8	110.8	124.0	117.8	123.5	127.0	131.5	136.1	136.7
99.6	116.2	111.1	121.2	118.2	124.7	127.0	133.8	141.1	143.1
100.5	118.9	111.7	126.0	118.7	121.9	127.1	130.9	-------	------

TABLE 2.—*Length (mm.) of 392 sea scallops when tagged* (L_g) *and released at latitude 41°52′ N., longitude 66°23′ W., on Sept. 22, 1957, and when recaptured* (L_r) *about 1 year later*—Continued

SAMPLE 3, OUT 60.7 WEEKS

L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r
85.5	106.0	99.3	113.2	108.3	123.3	117.7	122.7	127.1	131.7
90.4	106.8	100.8	114.3	109.7	117.0	119.1	128.8	129.8	131.9
93.0	109.4	102.1	111.5	110.7	121.2	120.8	127.8	130.4	132.9
94.8	111.0	102.1	116.5	110.9	117.2	121.5	126.5	133.1	137.6
96.3	114.9	104.8	117.3	111.4	116.8	121.9	126.3	133.3	136.0
97.7	113.9	104.9	118.2	112.9	125.9	123.4	131.4	133.9	137.1
97.8	119.6	105.5	119.8	113.0	119.8	123.9	129.9	135.4	140.1
98.0	110.0	106.4	118.1	114.2	126.5	124.6	131.7	135.9	137.3
99.0	106.5	108.2	124.4	116.0	124.0	126.7	130.1	147.3	147.7
99.0	115.7	-------	-------	-------	-------	-------	-------	-------	------

SAMPLE 4, OUT 64.1 WEEKS

L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r
86.2	110.3	99.3	120.8	109.2	123.3	116.4	123.3	125.4	131.4
87.6	107.3	99.7	118.3	109.3	115.5	116.4	125.1	127.5	131.6
88.9	110.9	99.7	118.5	109.9	119.6	117.9	125.7	128.9	130.8
90.2	110.0	100.5	113.1	110.9	120.3	118.4	125.2	129.1	136.5
93.1	117.3	101.2	117.0	111.5	122.9	119.2	125.2	129.2	134.6
93.5	115.6	101.3	118.1	111.5	123.5	120.5	131.4	129.7	134.4
93.9	113.3	104.1	121.0	111.6	124.0	121.3	133.6	130.3	132.5
95.9	114.0	104.3	119.5	111.9	123.0	122.0	128.5	133.3	140.2
97.4	114.0	105.1	120.7	113.3	122.4	122.5	132.4	136.6	138.3
97.6	114.3	105.7	121.5	113.9	122.8	122.9	128.2	137.9	139.0
97.6	121.8	106.0	118.5	115.5	119.3	123.4	129.2	138.4	140.1
98.2	113.2	107.6	112.9	115.7	124.1	123.8	129.2	143.7	145.5
98.5	108.1	108.4	117.4	-------	-------	-------	-------	-------	------

SAMPLE 5, OUT 66.7 WEEKS

L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r	L_g	L_r
86.8	104.8	104.2	116.2	111.5	126.1	117.9	125.1	128.5	130.1
92.2	117.9	105.7	119.2	112.9	121.1	120.9	130.6	128.6	130.5
93.1	114.5	105.9	115.3	114.2	126.5	121.0	128.8	129.5	131.0
94.8	117.5	106.7	119.2	114.9	121.7	122.1	127.7	129.7	131.1
95.1	116.2	107.6	123.3	115.1	120.4	122.3	128.0	129.8	132.7
95.1	117.7	107.8	120.1	115.2	127.5	123.5	127.4	130.3	134.0
98.6	115.3	109.3	120.3	115.3	126.7	124.7	127.7	130.4	136.8
100.1	113.3	109.4	120.6	116.7	124.9	125.6	133.2	136.7	138.2
100.8	116.0	110.2	119.2	116.8	123.9	126.9	132.2	139.3	140.2
100.8	116.8	110.3	127.5	117.2	128.9	127.0	137.5	141.8	143.7
100.9	113.0	110.4	124.2	117.8	125.5	128.2	132.4	149.3	150.1

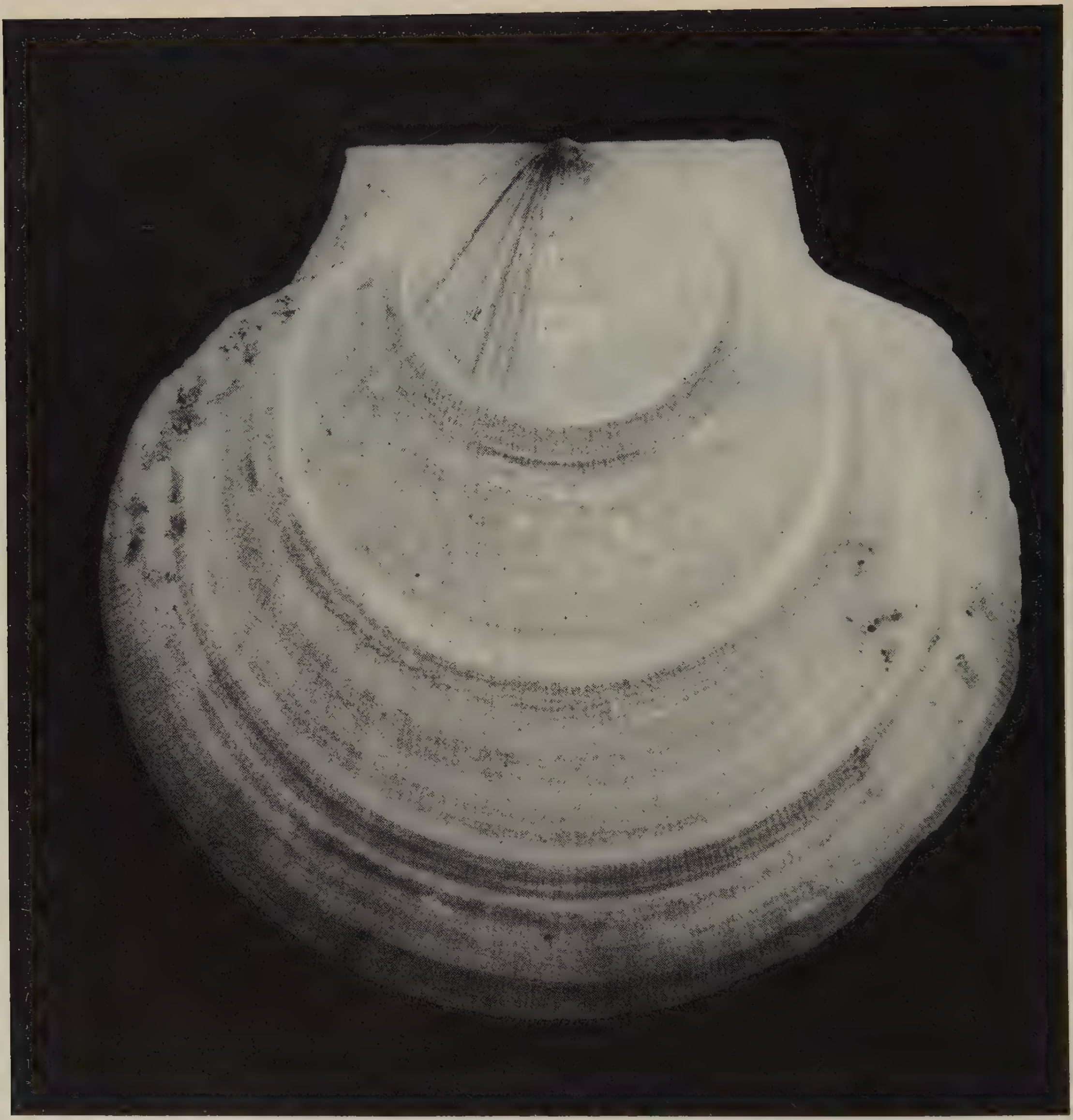

FIGURE 11.—Upper valve of a sea scallop showing seasonal change in color.

We have calculated the length at age for the 4 years following recruitment of sea scallops to the fishery using both growth-rate equations.

Item	Age				
	t	$t+1$	$t+2$	$t+3$	$t+4$
Equation 2	85.0	103.7	116.1	124.3	129.7
Equation 1	85.0	102.4	114.7	123.4	129.5

It is clear that the two equations, derived by different methods, give essentially the same results. We, therefore, have confidence in growth rates calculated by either method, and that our methods of locating annual rings are valid.

AGE AT RING FORMATION

It is interesting to note that, despite the strong check mark put on the shell at time of tagging, the tags apparently did not inhibit growth. Also, if we assume that there is little seasonal variation in the growth rate on Georges Bank, for those scallops that had been out for about a year, we can estimate the time of year when the annual ring is laid down from the position of the ring on the shell between the check mark made at time of tagging and the margin. On this basis, the 1958 ring appears to have been laid down about 27 weeks after the date of tagging. This places ring formation at March 30, just 6 months after October 1, which is the usual date of spawning by sea scallops in this area (Posgay and Norman, 1958). The true age at the time of ring formation in this area is, therefore, the number of the ring minus one-half year. There is a possibility, now under investigation, that the first definable ring, at about 20 mm., is not laid down during the first year of life but rather in the second.

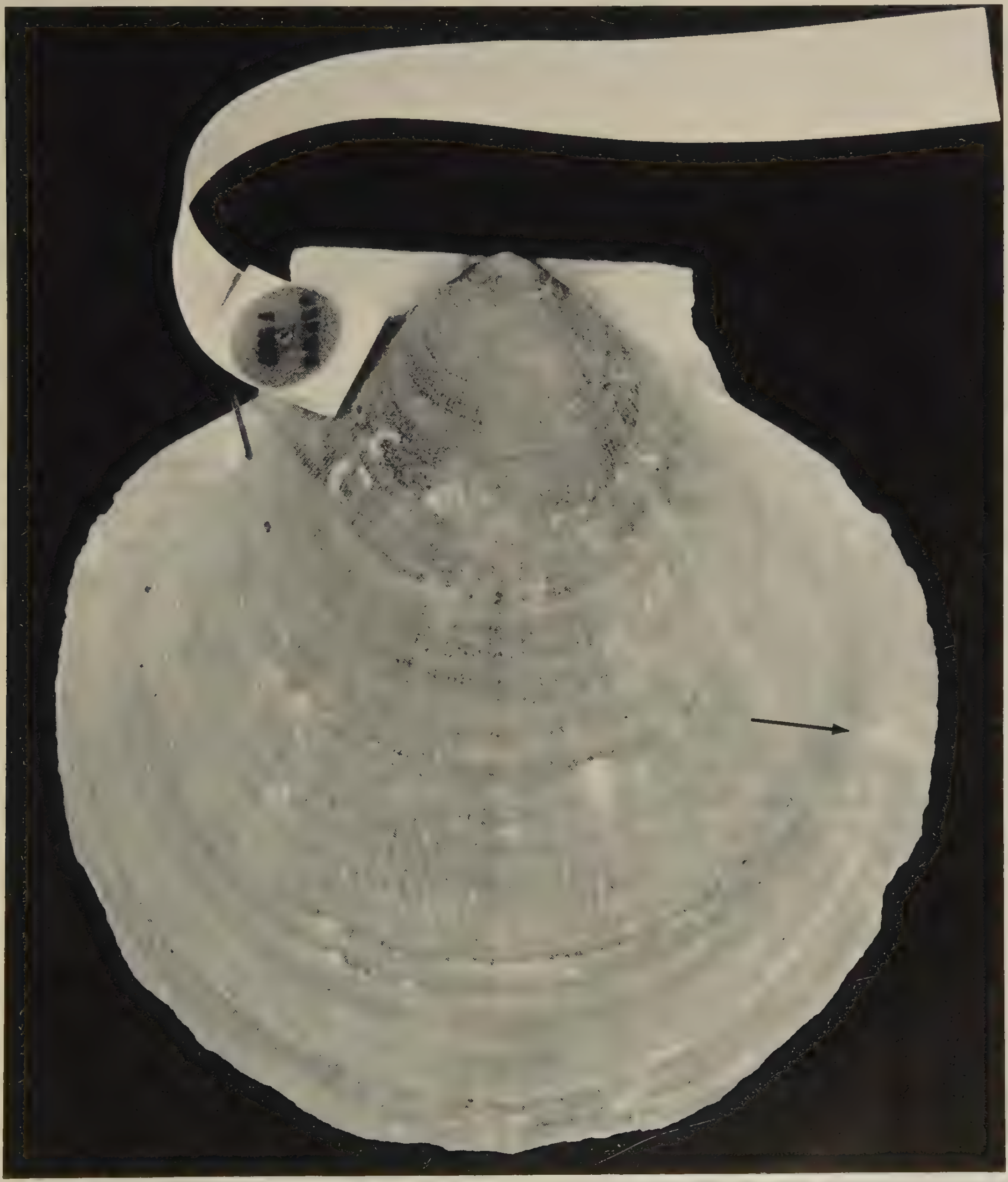

Figure 12.—Upper valve of a sea scallop that has been tagged, released, and recaptured. (The arrow points to the nick which was made in the margin at the time of release.)

TABLE 3.—*Age structure and average length (mm.) at time of ring formation in sample of 351 sea scallop shells determined independently by 2 readers*

Number of rings on the shells	Average length							Grand average
	3	4	5	6	7	8	9	
Reader No. 1:								
Ring number								
1	21.6	20.4	19.6	19.8	19.6	18.0	17.9	19.6
2	58.3	54.6	53.9	55.4	55.2	53.2	54.7	55.0
3	84.5	80.8	79.9	83.4	81.0	81.3	80.1	81.6
4	---	95.9	96.0	99.3	98.3	100.9	95.9	97.7
5	---	---	106.9	109.9	110.3	113.3	109.2	109.9
6	---	---	---	116.8	117.6	122.4	117.9	118.7
7	---	---	---	---	123.0	128.1	125.4	125.5
8	---	---	---	---	---	131.2	131.5	131.3
9	---	---	---	---	---	---	133.8	133.8
Number in ring group	85	71	75	57	37	17	9	---
Reader No. 2:								
Ring number								
1	21.2	20.5	20.0	19.7	19.7	19.9	18.2	19.9
2	56.1	53.2	53.8	55.0	54.9	51.5	54.9	54.2
3	85.8	83.5	81.2	82.5	81.2	79.7	80.8	82.1
4	---	98.7	98.3	99.8	98.6	98.7	97.7	98.6
5	---	---	109.2	111.9	110.6	110.5	109.1	110.3
6	---	---	---	118.6	118.4	120.4	118.4	118.9
7	---	---	---	---	123.8	126.7	125.6	125.4
8	---	---	---	---	---	130.1	131.5	130.8
9	---	---	---	---	---	---	133.5	133.5
Number in ring group	93	87	66	47	34	12	12	---

OBJECTIVITY OF THE CRITERIA

To test whether our criteria for determining which annuli were annual rings were sufficiently objective, a summer assistant, William Evoy of Reed College, was trained in the reading technique. He was then given a sample of 351 shells to age and measure, after which the same sample was read by the senior author.

The correspondence of results was very good (table 3). There was disagreement on the number of rings, but never by more than one, on about 10 percent of the shells and a few additional disagreements as to position of the annual ring. The growth-rate equations calculated from the two sets of data were virtually indistinguishable, as shown in the following formulae:

$$L_{t+1}=37.49+0.7384L_t$$

$$L_{t+1}=36.75+0.7467L_t$$

SUMMARY

The shell of the sea scallop, in common with many other mollusks, bears annual rings but they are frequently weak and ill-defined or masked by the presence of other annuli caused by nonannual phenomena. By using annual marks on the resilium, changes in shell curvature, changes in color pattern, weight of the shell, and areas of attack by boring organisms it is usually possible to localize the position of the annual rings so that they can be found by intensive examination.

These methods have been validated by showing that a growth rate calculated from the annual rings was almost identical with a growth rate calculated from the growth of tagged and recaptured animals from the same area.

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DYNAMICS OF A PENAEID SHRIMP POPULATION AND MANAGEMENT IMPLICATIONS

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ABSTRACT

In assessing present utilization of a stock of pink shrimp (Penaeidae) that supports an important commercial fishery in the eastern Gulf of Mexico, the interaction of population growth and mortality is critically analyzed. Estimates of the parameters involved were secured through a mark-recapture experiment wherein a biological stain served as the marking agent. The experiment was oriented in space and time so that exploitation of the marked population, which initially consisted of individuals uniform in size, provided measures of growth and mortality in the parent age group during and immediately following its transition from prerecruit to postrecruit status. Throughout the experiment, the entire stock as well as the marked population were heavily fished. Upon examining the question of whether or not the fishery's production could be improved by postponing the start of fishing until the shrimp reach a size greater than the 70 headless-count designation now generally viewed as a practicable minimum, it was noted that expected growth, although relatively high, would be insufficient to offset substantial losses due to expected natural mortality. Even with a moderate increase in growth rate, an appreciably reduced natural mortality would have to be indicated before such a move could be considered feasible. Maximum potential yield in both weight and value is obtained with the minimum acceptable size that the fishery currently imposes.

Broadly speaking, the basic goal of biological research undertaken by the Bureau of Commercial Fisheries is to gain the best possible understanding of how fishing and the principal environmental factors (once they are determined) govern the size of commercial fishery resources, and hence the yield of fish and fishery products. Its attainment would, theoretically, enable us to establish guidelines for maintaining any resource at about that level where production or, perhaps, economic advantage is highest. One should not gain the impression, however, that such a level can be held static over long periods of time, but recognize instead that it is subject to fluctuation from year to year in response to an everchanging environment and thereby presupposes continual readjustment of fishing intensity.

Utilization is associated very closely with the concept of resource maintenance. In the con notation of the phrase "conservation of natura resources," maintenance and utilization are, in fact, not mutually exclusive. But it is always likely that long before research can produce a scheme for effective resource maintenance, it will provide ad interim some indication of how a resource should be best utilized. Fishery research, which largely embraces the field of population ecology (including dynamics), becomes most efficient when it programs for short-term or intermediate as well as long-term objectives. It is noteworthy that the processes of achieving both types of objectives very often require the same basic data.

For nearly as long as Gulf of Mexico shrimp resources have been exploited, concern has prevailed as to whether they have always been utilized to best advantage. Many believe that the minimum size of commercially acceptable

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Note.—Approved for publication December 21, 1962.

shrimp should be increased, that the harvesting of any age group (or "brood") should be delayed until, by virtue of a high growth potential, maximum (or at least a greater) weight or biomass is reached. Phrased more simply, the question posed and heretofore not answered satisfactorily is: At what size per individual should an age group of shrimp begin to be harvested so as to realize the maximum yield from that group during its life span?

This question has important economic implications and requires that we understand the relationships between, and can measure, the rates of two concurrent biological processes: (1) *Growth*, the increase in shrimp size per individual per unit time, and (2) *mortality*, the numbers of shrimp dying per unit time (particularly due to natural causes).

Over the years, fishery biologists have found population growth and mortality parameters highly elusive. Recently, however, as part of its long-range shrimp research program, the Bureau of Commercial Fisheries perfected a very satisfactory process of marking shrimp that now permits such parameters to be approximated by the useful mark-recapture technique. The marking system proving so successful is the stain-injection method. Menzel (1955) is generally credited as having conceived its use on shrimp; Dawson (1957) as having substantiated its potential by means of laboratory experimentation; and Costello (1959, 1964) and Costello and Allen (1960) as having developed its large-scale application afield.

This paper first presents the results of a mark-recapture experiment with a rather well-defined stock of pink shrimp, *Penaeus duorarum* Burkenroad, which supports an important commercial fishery in southwest Florida, the widely known Tortugas fishery. After documenting the required estimates of growth and mortality, the paper then describes their synthesis through a theoretical yield equation to attempt an answer to the question stated earlier. In so doing, it draws in small part on the results of yet another mark-recapture experiment conducted with the same species, but for a different purpose, just prior to the one of primary interest.

Though it was classified as merely preliminary and expanded efforts were to be scheduled only if it achieved any reasonable degree of success, the Tortugas experiment proved successful well beyond our somewhat modest expectations. The quality of the resulting data is reflected in the kind of treatment they are given here. Such extensive treatment, regardless of the experiment's outcome, had not been anticipated in advance.

TORTUGAS MARK-RECAPTURE EXPERIMENT

DESCRIPTION AND REGULATION OF FISHERY

Lying west of Key West, Fla., reaching little beyond the 30-fathom contour, and extending not much farther northward than the 25th parallel, the Tortugas trawling grounds seasonally experience some of the most intense shrimp fishing seen in the Gulf of Mexico (fig. 1). Stimulating this activity is the appearance of large numbers of subadult pink shrimp which emerge in closely spaced surges from the shallow "nursery" grounds in Florida Bay to the east.[1] Although maturing shrimp may enter the fishing grounds at all seasons, it is in September-March that migrations are greatest and fishing is heaviest. Practically all fishing occurs at night when the pink shrimp is most active and hence most vulnerable. Like its close relative the brown shrimp, *P. aztecus* Ives, this species usually burrows and is therefore comparatively inaccessible during the hours of daylight.

Most trawlers operating on the Tortugas and adjacent grounds are of the characteristic Florida design (fig. 2). For all practical purposes they are nearly uniform in size and power, and employ fishing gear of roughly the same specifications (Iversen and Idyll, 1959; Kutkuhn, 1962).

The Tortugas fishery together with a lesser one, the Sanibel fishery, which is centered roughly 100 nautical miles to the north, did not become well established until the early 1950's (Idyll, 1957). A question often raised and now being examined is whether populations supporting both fisheries are genetically discrete, or whether they are continuous—even though continuity may prevail only at widely spaced life history stages. Evidence acquired to date tends to support the assumption made in this study that the Tortugas fishery largely depends on a stock of pink shrimp which is essentially separate from that sustaining the Sanibel fishery (Costello and Allen, 1960; 1961).

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[1] Idyll (1957), Dobkin (1961), and Cummings (1961) should be consulted for a detailed account of pink shrimp life history.

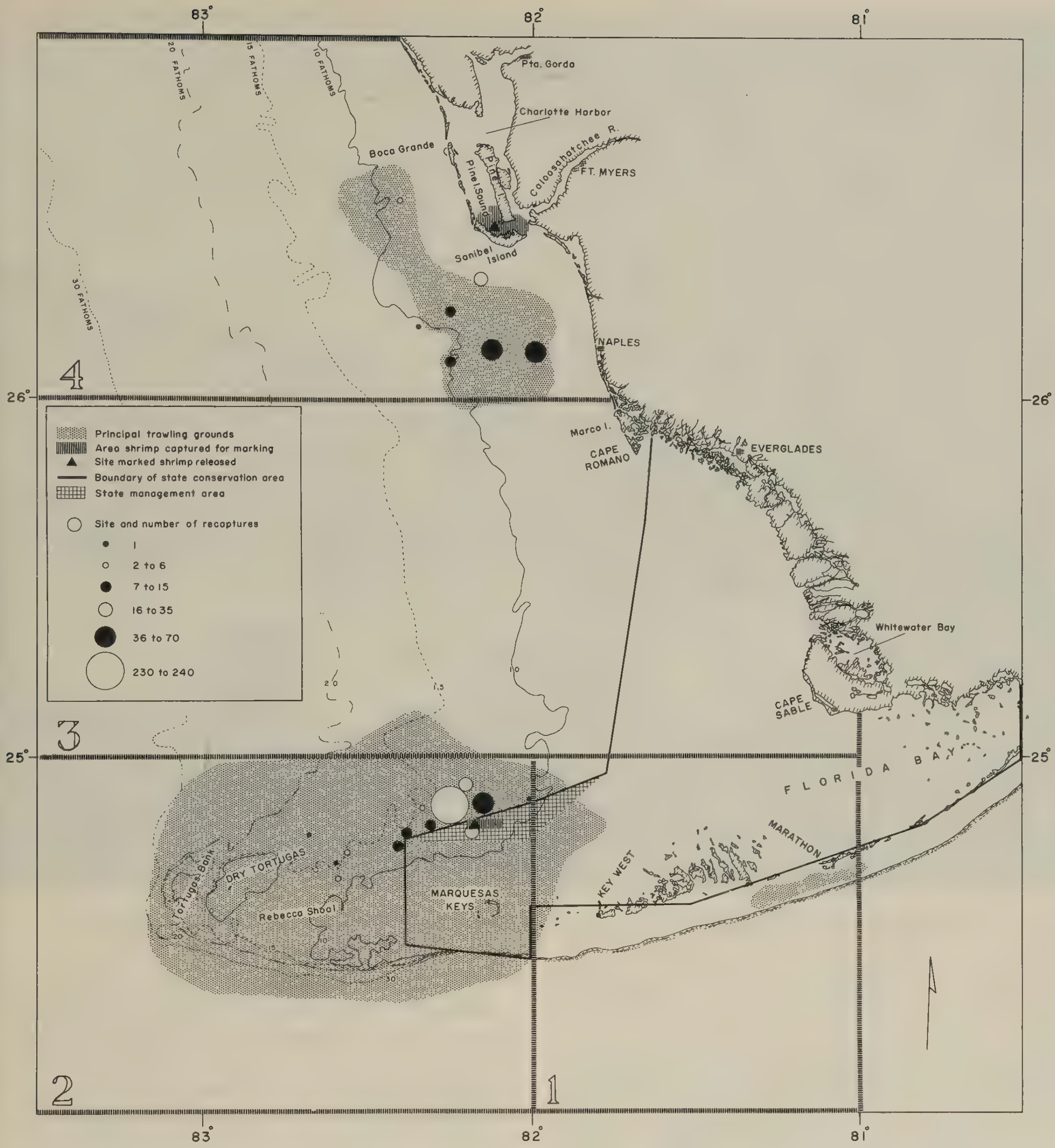
83°
82°
81°
20 FATHOMS
15 FATHOMS
10 FATHOMS
30 FATHOMS
Pta. Gordo
Charlotte Harbor
Caloosahatchee R.
Boca Grande
Pine I.
Pine Island Sound
FT. MYERS
Sanibel Island
NAPLES
4
26°
Marco I.
CAPE ROMANO
EVERGLADES
Principal trawling grounds
Area shrimp captured for marking
Site marked shrimp released
Boundary of state conservation area
State management area
Site and number of recaptures
1
2 to 6
7 to 15
16 to 35
36 to 70
230 to 240
Whitewater Bay
CAPE SABLE
3
25°
FLORIDA BAY
MARATHON
KEY WEST
DRY TORTUGAS
Tortugas Bank
Rebecca Shoal
MARQUESAS KEYS
2
1

FIGURE 1.—General area in which mark-recapture experiments were conducted. Large numerals (1–4) identify coastal subareas employed in tabulating fishery statistics. Data shown in subarea 2 refer to the Tortugas experiment (September–December 1961), those in subarea 4 to the Sanibel experiment (December 1960–June 1961).

Annually contributing about 10 percent to the total Gulf production of shrimp, landings in the Tortugas fishery reached a peak of 23.6 million pounds in 1960, having risen from almost a record low of 12.9 million pounds the year before. The latter value represented a 44-percent drop from the previous high of 23.0 million pounds landed in 1958.[2] Since 1956 the fishery has seemingly had

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[2] Source: Gulf coast shrimp data, published monthly by the Branch of Fishery Statistics, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.

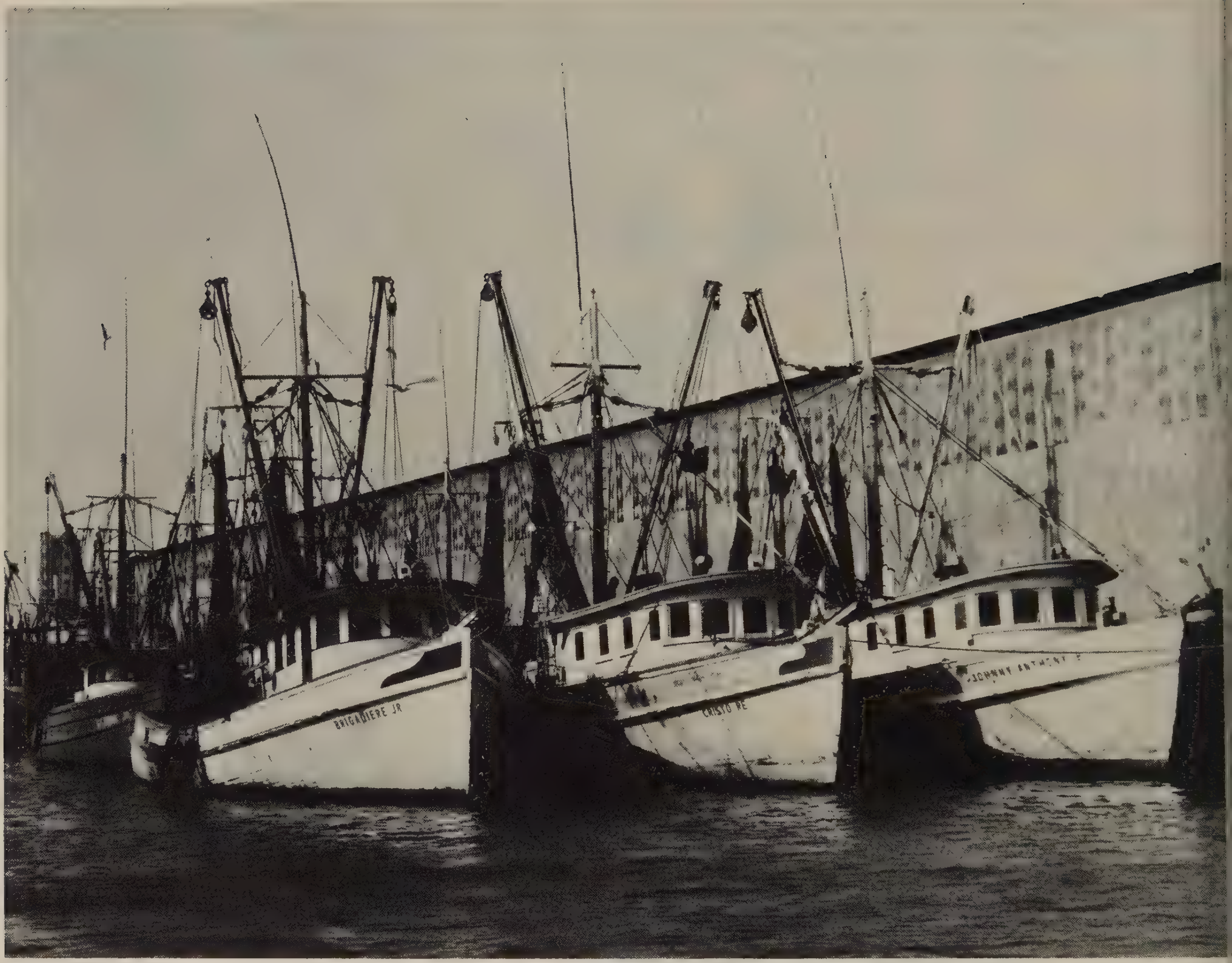

FIGURE 2.--Double-rigged, Florida-type trawlers predominate in the Gulf of Mexico shrimp fleet.

to rely to an increasing extent on small shrimp to keep production at a profitable level (Kutkuhn, 1962).

Believing that utilization might be improved by inhibiting the harvest of small shrimp, the Florida State Board of Conservation established in 1957 what is called a "control" area (Ingle, Eldred, Jones, and Hutton, 1959, figs. 1–3). This area was so situated that the preponderance of shrimp entering the open fishing grounds ostensibly migrated through it. Fishing was not to be permitted in the control area whenever periodic surveys disclosed that the shrimp therein were smaller than the size at which 50 headless and uniformly sized individuals weigh 1 pound. This regulatory concept was revised in mid-1961 when the Board delineated a permanently closed conservation area which incorporated part of the earlier control area and extended the latter's boundaries to enclose all of Florida Bay (fig. 1). Also circumscribed was a less extensive management (control) area from which only shrimp of 60 "headless-count" or larger may be taken.

MARKING PHASE

The Tortugas mark-recapture experiment was designed to take complete advantage of the physical and regulatory features of the fishery. Shrimp destined to make up the experimental population were to be captured, marked, and released just prior to the onset of heaviest expected fishing intensity. Concentrations of precommercial-size shrimp moving through the State management area offered the opportunity to establish an experimental population from which could be obtained measures of growth and mortality in the parent population before and during as well as after its transition from prerecruit to postrecruit status.

Accordingly, operations using facilities provided by the Bureau's M/V *George M. Bowers* got underway on September 18, 1961, with the first releases of marked shrimp being made 2 days later. Shrimp were captured with small-mesh trawls hauled for very short intervals of time (frequently not more than 2 minutes) to minimize injury caused by compression in the net. To insure that only shrimp in prime condition entered the experiment, catches were held in tanks of circulating sea water for periods of at least 12 hours. After all weak and dying individuals had been removed, the remainder was sorted so that only those falling into a specified size range (total length) were retained for marking. This range was arbitrarily set using as a point of reference the modal length of available shrimp, such length having been determined by sampling catches made at the start of operations. Graded individuals were then marked by carefully injecting small quantities of a 0.25-percent aqueous solution of Trypan blue stain. Groups of marked shrimp were observed for at least 4 hours before being released, only the most vigorous individuals at the end of that time being selected for the experiment. These were released in lots of 100 at scattered sites and at irregularly spaced intervals during the marking period by means of a special release box (Costello, 1964). This device permitted the experimental shrimp to be returned directly to the bottom from whence they came (the depth being about 12 fathoms), and precluded large-scale losses due to predation by fishes and birds that would have occurred had the shrimp been released at the surface. Underwater movies taken during this operation reveal that marked shrimp released from the box immediately burrowed into the bottom, thereby satisfying the assumption that predation losses were, for all practical purposes, nonexistent. Because of judicious handling, selection, and release of the experimental material, it is hereinafter assumed that the total number of marked shrimp reintroduced into the parent population represented the actual or "effective" size of the marked population established during the marking period.

In the manner just described, an experimental population of 2,090 individuals was created within a 4-day period. Figure 1 shows the general location of capture and release sites. Measurements from an accumulation of small samples drawn each time a group of shrimp was released provided essential information concerning the population's length and weight attributes at the start of the experiment (table 1).

COMMERCIAL FISHING OPERATIONS DURING EXPERIMENT

Greatly influencing the outcome as well as the utility of results of experiments like the present one are the amount and distribution of recapture effort relative to the distribution of the experimental population. With all other potential sources of bias inoperative or satisfactorily accounted for, the rate at which marked individuals are recaptured becomes simply a function of the probability of recapture.[3] An index of this probability is, logically, the intensity of fishing or, in a rather restricted area such as is involved here, the fishing effort. A major problem is that the fishing effort often does not remain constant and thereby confounds the probability of recapture. It must be assumed at the outset, of course, that the experimental population soon reintermingles with and behaves in the same manner as the parent population (age group) from which it was temporarily removed.

Detailed information of fishing operations during the Tortugas experiment was provided by the Bureau of Commercial Fisheries Branch of Fishery Statistics which has agents stationed at major Gulf ports, including Key West, Fort

TABLE 1.—*Sex, length, and weight data from samples of the marked population at the beginning of the Tortugas experiment, middle of week ending Sept. 23, 1962*

[Number in marked population: 2,090. Estimated sex ratio: 60♂:40♀]

Sex	Number sampled	Carapace length[1]		Total length		Total weight	
		Mean	Range	Mean	Range	Mean	Range
		Mm.	*Mm.*	*Mm.*	*Mm.*	*G.*	*G.*
Male	168	19.2	17.9–20.1	90.1	84.2–94.1	5.9	4.8–6.8
Female	110	19.5	18.5–20.2	88.9	84.2–94.1	6.0	5.2–6.7
Total	278	19.3	17.9–20.2	89.6	84.2–94.1	5.9	4.8–6.8

[1] Carapace length is defined as the straight-line distance from the posteromost edge of the orbit to the posterior edge of the carapace where it intersects the middorsal line.

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[3] Throughout this report, "recapture" refers to the marked shrimps' capture by the fishing gear; in contrast, "recovery" refers to their subsequent detection in commercial catches (or landings).

Myers, and Tampa, Fla. Estimates of the total effort expended weekly on the Tortugas grounds had to be projected from sample interviews (n) with trawler captains landing their catches at these ports. The procedure simply consisted of estimating from the sample data the average number of hours fished during each fishing trip and multiplying this by the total number of trips as determined by a canvass of processing plant records. Thus, the total hours fished in any week is given by

$$\hat{X}=N\bar{x}=\frac{N}{n}\sum_{1}^{n}x_i \qquad i=1, 2, 3, \ldots n$$

where N is the total number of trips by individual trawlers to the fishing grounds, x_i is the number of trip-hours fished as reported by the captain of the i^{th} vessel entering a weekly sample, and $\bar{x}=\frac{\sum_{1}^{n}x_i}{n}$ is the sample estimate of the mean number of hours actually spent fishing during each trip. The only difficulty arose when "uninterviewed" trips ($N-n$) extended over periods of more than 1 calendar week. In such cases, fractional trips for each of any 2 adjoining weeks had to be designated. These fractions were then summed together with trips contained entirely within respective weeks to obtain the weekly totals. Variances of the sample estimates were also calculated and, under the assumption of negligible or constant sampling bias, provided the estimates of total effort with an index of reliability. Hence

$$v(\bar{x})=\frac{\sum_{1}^{n}(x_i-\bar{x})^2}{n(n-1)}\left(\frac{(N-n)}{N}\right)$$

and

$$\text{confidence interval } (\hat{X})\text{: } \hat{X}\pm tN\sqrt{v(\bar{x})}$$

where t is the value of the normal deviate corresponding to the desired confidence probability.

The Tortugas experiment lasted about 14 weeks; table 2 gives effort statistics and estimates, together with total landings, for each week plus the two that immediately preceded the start of the experiment. To provide some indication of how the effort was distributed on the fishing grounds, the weekly totals are also apportioned (on the basis of interview data) among three well-defined depth zones. Landing figures are not estimates but accumulations of actual catch weights obtained through a continuing canvass of all processing plants.

One other matter that will warrant consideration in a later section relates to the stage in age group development at which the member shrimps' commercial acceptance becomes complete, or selectivity no longer constitutes a factor. As employed here, the word "selectivity" does not refer to the selective properties of fishing gear but means, rather, the purposeful avoidance of shrimp of undesirable size even though they may be largely vulnerable to the gear in general use. Such selection is ordinarily accomplished by sorting catches or by test fishing for aggregations in which most individuals are of marketable size.

Unfortunately, the minimum marketable size of shrimp varies within the industry (or according to State law) from area to area around the Gulf and in some localities may be only vaguely defined (or not stringently enforced). During the Tortugas experiment the fishery did not recognize a specific minimum size, with the result that sorting catches for the purpose of discarding small shrimp was not practiced. In fact, the only form of selection evident was the weekly expenditure of comparatively small amounts of fishing effort prior to the period in which the greater proportion of available shrimp reached a size of about 70 headless-count.

Examination of size (weight) frequency curves obtained from landings during the study period disclosed that selective fishing solely for medium and large shrimp was, practically speaking, inoperative (fig. 3). It suggested further that shrimp somewhat below the size designated herein as the minimum acceptable size (70 headless-count) were, if not entirely, almost wholly vulnerable and actively sought out by a sizeable though undetermined portion of the fishing fleet. Figure 3 clearly shows that small (in many instances, very small) shrimp predominated in Tortugas catches during the last 15 weeks of 1961. This fact lends credibility to the assumption that bias due to the selective action of the fishing gear was negligible and that the retrieval of marked shrimp of a size well below that tacitly set as a commercial minimum was almost entirely governed by the probability of a piece of gear encountering and capturing them, even though such probability

TABLE 2.—*Commercial shrimping operations in Gulf of Mexico statistical subareas 1-3 (Dry Tortugas-Marquesas) during September–December 1961*

Item	Week ending							
	9-9	9-16	9-23[1]	9-30	10-7	10-14	10-21	10-28
Total number of trips (N)	41	77	81	88	80	88	35	115
Number of trips sampled (n)	7	15	21	19	23	27	16	26
Mean number of hours fished per trip ($\bar{x}$)	28.8	35.8	26.0	31.8	49.7	32.1	26.2	32.9
Variance of mean $v(\bar{x})$	22.0	10.8	5.8	20.1	8.1	6.9	5.8	3.1
Coefficient of variation	0.16	0.09	0.09	0.14	0.06	0.08	0.09	0.05
Estimated total effort in hours ($\hat{X}$)[2]	1,180±250	2,760±330	2,110±250	2,800±510	3,980±290	2,820±300	920±110	3,780±270
—at: 0-10 fathoms	-----	-----	-----	-----	-----	-----	-----	-----
11-20 fathoms	1,180	2,760	2,110	2,600	3,720	2,770	920	3,780
21-30 fathoms	-----	-----	-----	200	260	50	-----	-----
Percent of total effort in Subarea 3	1	1	1	9	5	7	3	10
Total landings[3]	42.1	287.9	301.6	212.2	227.3	179.9	72.8	411.8

Item	Week ending								
	11-4	11-11	11-18	11-25	12-2	12-9	12-16	12-23	12-30
Total number of trips (N)	97	206	270	177	175	201	217	161	67
Number of trips sampled (n)	20	62	97	69	37	53	74	48	2
Mean number of hours fished per trip ($\bar{x}$)	41.7	28.3	37.3	30.7	39.9	44.4	42.1	35.9	24.0
Variance of mean $v(\bar{x})$	12.1	3.2	3.2	3.7	10.0	6.3	3.0	3.3	23.3
Coefficient of variation	0.08	0.06	0.05	0.06	0.08	0.06	0.04	0.05	0.20
Estimated total effort in hours ($\hat{X}$)[2]	4,040±440	5,830±480	10,070±630	5,430±440	6,980±730	8,920±650	9,140±480	5,780±380	1,610±420
—at: 0-10 fathoms	-----	-----	-----	-----	-----	180	330	80	390
11-20 fathoms	3,680	5,600	8,760	4,890	6,840	8,060	7,820	5,380	1,190
21-30 fathoms	360	230	1,310	540	140	680	990	320	-----
Percent of total effort in Subarea 3	5	3	6	9	1	6	4	8	1
Total landings[3]	365.3	680.2	763.7	215.8	240.1	467.3	433.1	189.9	39.0

[1] Week in which experiment began.
[2] 0.80 confidence intervals.
[3] Thousands of pounds (whole shrimp).

was represented in part by purposively selective effort. It follows that the likelihood of recaptures being subsequently recovered from commercial landings had to be presumed essentially constant throughout the experiment regardless of shrimp size.

RECOVERY PHASE

Extensive publicity coverage preceded and continued during the experiment. With the assistance of the Bureau's Branches of Fishery Statistics and Market News, cooperation in the retrieval of stained shrimp was solicited through correspondence, market reports, and personal interview from all industry segments as well as from State conservation agencies and the Gulf States Marine Fisheries Commission. The press, radio, and television provided additional coverage. A reward of $2 was offered for the return of any marked shrimp when accompanied by information regarding its place and date of capture. Posters to this effect (fig. 4) were conspicuously placed in all processing plants adjacent to the area in which the experiment took place. Close contact with fishermen and processors was maintained at all times.

Return of marked shrimp began immediately with 47 having been recovered before the end of the experiment's first week, referred to herein as the "period of release." Fortuitously, the State management area in which the marked shrimp were released (fig. 1) was opened to commercial fishing 2 days after the experiment got underway. In all, 443 or 21 percent of the total number liberated were eventually recaptured and returned for verification.[4] Daily distribution of recaptures is shown in figure 5. To facilitate subsequent analysis, they are grouped by calendar weeks (top of fig. 5).

Recovery continued strong for the first 8 weeks, reaching a peak during the sixth week and then dropping sharply (fig. 5). No marked shrimp were recovered after the 13th week. This abrupt attenuation reflected a real decline in the experimental population since associated recapture (fishing) effort did not decrease but rose significantly. Emigration of marked shrimp from the range of effective fishing effort appeared negligible (fig. 1), with no individuals being taken beyond 20 fathoms (only two outside 15 fathoms) or north of the 25th parallel despite measurable expenditures of effort at both locations (table 2). In general,

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[4] One marked shrimp returned 3 months after recapture was not included in subsequent analyses.

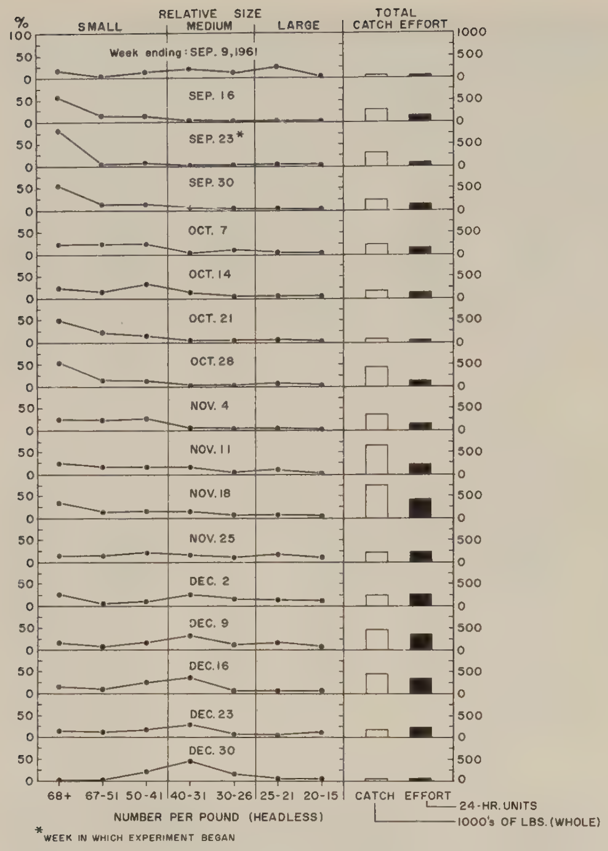
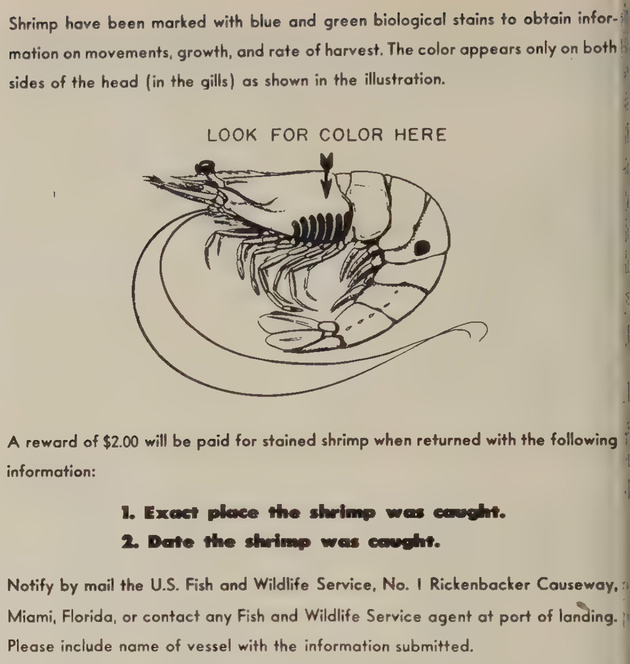


FIGURE 3.—Weekly commercial catch and effort statistics from the Tortugas pink shrimp fishery (statistical Subareas 1–3), September–December 1961.

what little movement was observed for the marked shrimp during the course of the experiment seemed to be in a west-northwesterly direction. As will be shown later, the week in which most marked shrimp were recaptured (sixth week, October 22–28) coincided with that during which the preponderance of the experimental population attained the "minimum" commercial size designated earlier. In other words, selective fishing by a heretofore undetermined portion of the fishing fleet ceased to be a factor at approximately this point.

Slightly less than three-fourths of the marked returns were detected while handling catches at sea. Because of the consistently small size of shrimp taken during the experiment (fig. 3), the great majority of catches had to undergo complete processing ashore. Such treatment entailed removing the head of each shrimp by hand, an


Shrimp have been marked with blue and green biological stains to obtain information on movements, growth, and rate of harvest. The color appears only on both sides of the head (in the gills) as shown in the illustration.

LOOK FOR COLOR HERE

A reward of $2.00 will be paid for stained shrimp when returned with the following information:

1. Exact place the shrimp was caught.
2. Date the shrimp was caught.

Notify by mail the U.S. Fish and Wildlife Service, No. 1 Rickenbacker Causeway, Miami, Florida, or contact any Fish and Wildlife Service agent at port of landing. Please include name of vessel with the information submitted.

FIGURE 4.—Typical poster advertising reward for the return of marked shrimp. Blue stain was employed in both the Tortugas and Sanibel experiments.

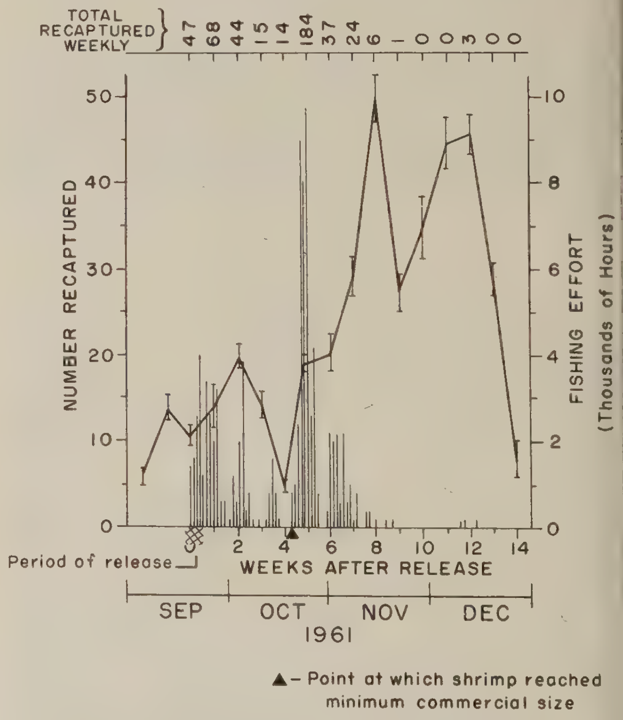


FIGURE 5.—Temporal distribution of fishing effort and of marked shrimp recaptured during the Tortugas experiment. Vertical bars from the abscissa represent number recaptured on indicated days. Vertical lines through points on effort curve define 0.80 confidence intervals for weekly effort estimates.

operation usually undertaken aboard the fishing vessel when most of the catch consists of medium-size or larger shrimp. Regardless of where beheading takes place, however, the chances of detecting marked specimens in the process are always very good to excellent. Under the conditions prevailing in most processing plants they are highest. All recovered shrimp not found at sea by vessel crews were later retrieved by plant personnel.

So far as is known, only a small fraction of all landings made within the study period escaped such close scrutiny, this occurring when landings infrequently had to be shipped directly to canneries located on the northern Gulf coast.

SANIBEL MARK-RECAPTURE EXPERIMENT

Though specifically designed for another purpose, the Sanibel experiment yielded growth data that proved useful in corroborating comparable data derived from the Tortugas experiment. By way of providing a brief description, the former experiment began about 9 months before the latter and extended over the period December 1960 to June 1961. In an attempt to determine the migration patterns of juvenile pink shrimp as they leave estuaries in the vicinity of Sanibel Island, Fla., 32,900 shrimp were marked with Trypan blue stain and released in Pine Island Sound. Commercial fishermen subsequently recaptured 155 (or 0.5 percent) at the locations indicated in figure 1.

Individuals making up the experimental population were first graded to uniform size though not nearly so carefully as those selected for the Tortugas experiment. A sample of 463 specimens taken at the experiment's start revealed a mean total length and corresponding weight of 75.3 mm. and 3.5 g., respectively. Sexes occurred in the estimated ratio of 46 males to 54 females.

ESTIMATION OF GROWTH

METRIC CONVERSIONS

Solution of the yield equation employed in a later section postulates that the average growth of each individual making up the population of interest be expressible in terms of weight, and that the average relationship between an individual's weight and length be firmly established.

Since it is ordinarily impractical to measure precisely in the field the weight of animals as small as shrimp, sampled individuals for the most part must be measured as to length at the sampling site, or preserved (rarely frozen) and later measured, again according to some length criterion, at a more convenient time and place. Subsequently required in either case are appropriate means for converting length to weight units.

Three situations that are met in the course of studies like the present one, and in shrimp research generally, may thus be defined. The first entails reciprocal conversion of the linear size indices commonly used in shrimp work, viz, total and carapace length. In this study, for example, total length was the criterion used to grade shrimp selected for the Tortugas experiment. But the sample from which the actual size-range limits were determined had to be preserved (formalin) for later measurement under more favorable conditions. Since the total length of shrimp so treated cannot be accurately measured because of the distorting and hardening effects of the preservative, carapace length, which remains unimpaired, provides the most practicable index of shrimp size. The statistical relationship between total length and carapace length serves to transform either linear dimension to the other and proves particularly useful when comparing the results of research in which the methods of measurement differ from one study to the next.

The two remaining situations prevail where interest centers on the transformation of linear to weight units, i.e., (1) from total length to total weight when length measurements can be made at the time of sampling and (2) from carapace length to total weight when the sample material must first be preserved.

Over the period August 1960 to January 1961, and independent of the experiments reported herein, weight and corresponding length measurements were obtained from slightly more than 1,600 pink shrimp sampled from commercial catches taken along the east and southwest Florida coast (Biscayne Bay and the Tortugas-Marquesas area, respectively). An indication of their statistical strength in terms of sample distribution by sex and relative size is given in table 3.

TOTAL LENGTH-CARAPACE LENGTH RELATIONSHIP

A plot of the mean carapace lengths for each of 28 male and 36 female, 5-mm. total-length classes suggested that the relationship between the two attributes could be best described by a simple exponential (fig. 6). Up to a total length of about 150 mm. the relationship for both sexes appears nearly identical and is, for all practical purposes, rectilinear. Beyond this length, however, definite curvature indicates that increases in carapace length (c) do not keep pace with increases in total length (l). Note also in the larger shrimp a marked sex differential in the total length-carapace length ratio. Thus, for shrimp of the same total length, females will have a greater carapace length than males, the difference increasing with size.

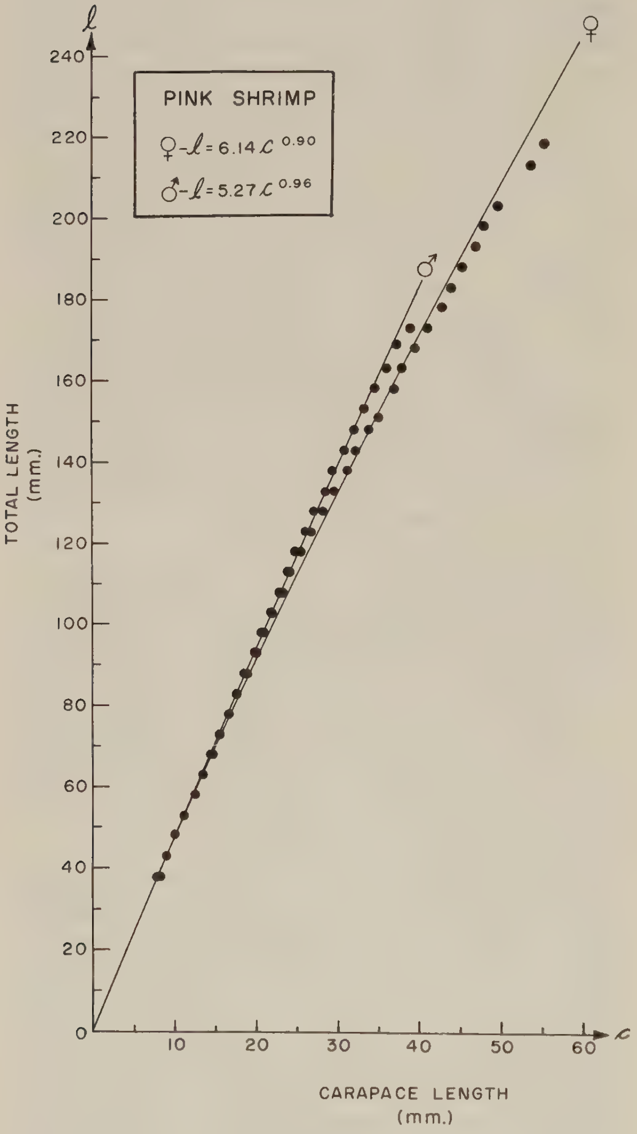


FIGURE 6.—Total length-carapace length relationship in pink shrimp.

TABLE 3.—*Distribution by sex and relative size of pink shrimp sampled during 1960–61 in south Florida for weight and length measurements*

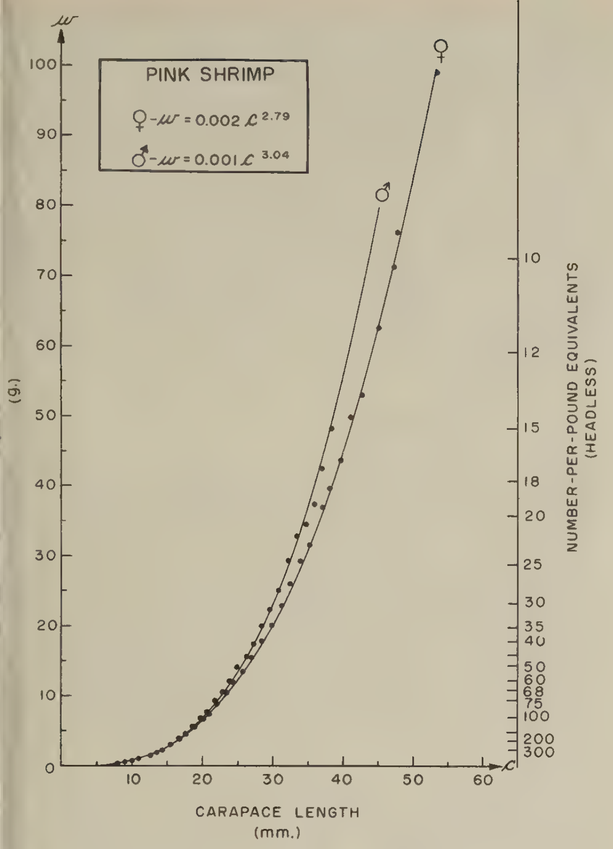
Sex	Number of specimens measured	Range in total length	Number of 5-mm. length classes	Average number of specimens per class	Number of classes with less than 15 specimens
		Mm.			
Male	729	35–175	28	25	3
Female	888	35–215	36	26	3
Total	1,617	35–215	36	45	3

For pink shrimp not exceeding 170 mm. total length (equivalent to 16 headless-count), the information provided in figure 6 will permit, graphically or mathematically, reasonably accurate estimation of total length from a known carapace length. Although precision diminishes somewhat above this limit, resulting estimates will still be sufficient for most purposes.

Linear conversions indicated in table 1 and elsewhere in this study employed the information given in figure 6.

Weight-Length Relationships

Plots of data categorized as above showed weight to be a simple power function of length. Either the fitted curves or equations for total weight (w) as a function of carapace length (fig. 7), and as a function of total length (fig. 8) may be used to estimate weight from either linear dimension with reasonable precision and accuracy. Close examination revealed some seasonal variation in the relationships, but not enough to be of practical significance. Sex differences are clearly evident in each case with the disparity being particularly prominent in the total weight-carapace length ratios. Among shrimp having the same carapace length, males, on the average, not only possess a greater total length but are heavier than females. It follows, conversely, that in individuals of the same total length, the males will weigh less than the females and have a shorter carapace. These differences should be borne in mind whenever metric conver-



IGURE 7.—Total weight-carapace length relationship in pink shrimp.

ons of the types treated here become necessary.

All length-to-weight conversions required in ubsequent analyses are made with the informa-on shown in figures 7 and 8.

Of particular interest in the present study is hether or not shrimp growth is isometric or, more pecifically, whether or not the total weight-total ngth relationships derived above conform to the ell-known cube law, viz., $w=al^b$, where $b=3$. onformation (or lack thereof) should be acknowldged when growth and mortality parameters are ntegrated to solve the yield equation referred to arlier and described in a later section. The fact hat the parameters of the mathematical expresons relating total weight to total length proved lmost identical for both sexes (fig. 8) simplified omewhat their statistical assessment. Upon eing tested with sexes separate or combined, the ypothesis of no exponents differing significantly rom $b=3$ had to be rejected. [For sexes comined—H_0:$b=3.00$ when in fact $b=3.14$—$t=11.16$, compared with $t_{.05}$ (33 degrees of freedom) $=2.04$.]

ESTIMATING GROWTH PARAMETERS AND FITTING CURVES

Recaptures from the Tortugas experimental population provided some of the best data yet obtained for describing growth in North American Penaeidae (table 4). In synthesizing these data for practical application later, a growth differential between sexes materialized as the only real impediment, there being no evidence of growth inhibition by the mark employed. Ideally, growth constants for both sexes should be treated separately (via summation methods) in all yield predictions, particularly since the maximum size attained by male shrimp appears to fall far short of that attained by females (*re* table 3). Whether or not both sexes have equivalent life expectancies poses still another argument that would have to be reconciled. But, to obviate undue complexity and because breakdown of recapture data by sex

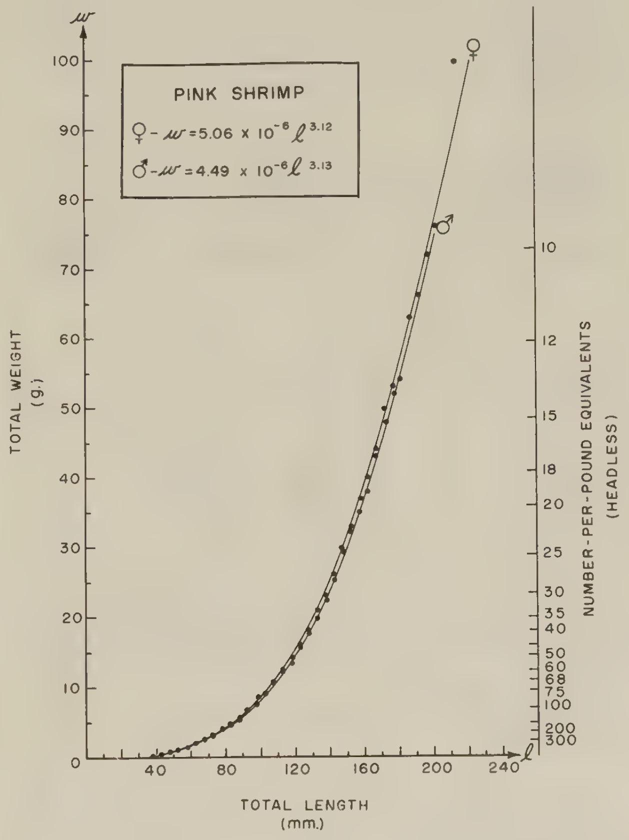


FIGURE 8.—Total weight-total length relationship in pink shrimp.

would have resulted in diminished reliability of sample length and weight estimates, each growth statistic hereinafter computed and substituted in yield equations reflects a compromise or "sexes-combined" situation. Although such statistics are in a sense artificial, their use is justified in that they define the average growth pattern within the experimental population during that period when the age group represented was enjoying greatest biomass, was most accessible, and its sex ratio had not yet begun to indicate a preponderance of females. Each estimate obtained may be viewed as lying intermediate between some upper value for females and a lower value for males.

It follows also that experimental length and weight data from a sexually heterogeneous population yield the most reliable growth-parameter estimates when the sex ratio of marked recaptures remains constant throughout the experiment. In the case of the Tortugas experiment, the sampling distribution of ratios generated over the period t_1-t_8 revealed no significant statistical departure when checked for goodness of fit against the uniform distribution theorized from the sex ratio established at the experiment's beginning [$\chi^2=12.15$ compared with $\chi^2_{.05}$ (6 degrees of freedom)$=12.59$].

Table 4.—*Mean lengths and weights of marked pink shrimp recaptured during successive weeks of the Tortugas experiment, September–December 1961 (sexes combined)*

Week of experiment t_i	Number recaptured[1] n	Distribution of males	Mean total length l	Mean weight w	Range in weight	Equivalent number per pound (headless)
		Percent	*Mm.*	*G.*	*G.*	
0	[2] 325	60	88.8	5.9	4.9– 6.6	123
1	68	51	90.0	6.1	4.9– 7.1	119
2	39	54	92.5	6.6	5.5– 8.3	110
3	15	47	103.9	9.5	8.0–10.2	76
4	11	61	106.0	10.2	8.1–11.3	71
5	176	55	109.8	11.4	7.5–15.8	64
6	35	42	113.1	12.5	10.1–18.3	58
7	22	67	118.7	14.5	9.6–17.6	50
8	6	67	123.2	16.2	13.4–19.2	45
9	[3] 1	100	123.4	16.4	----------	44
10	0	----------	----------	----------	----------	----------
11	0	----------	----------	----------	----------	----------
12	[4] 2	50	130.4	19.5	18.7–20.2	37

[1] Total number of recaptures used for growth computation (422) does not agree with total number recaptured during experiment (442) because breakage or other damage precluded carapace-length measurement in some (20) specimens.

[2] Data from 47 recaptures combined with sample data (table 1) secured during period of release.

[3] Measurements from this specimen excluded from growth computation.

[4] One other specimen (♀) returned 3 months after recapture was not included in analysis.

Although comparable growth data contributed by the Sanibel experiment did not meet the requirement of constant sex ratio (table 5), their greater temporal range gave a better indication of the probable shape of the pink shrimp growt curve. Subsequent plots of mean weights c marked shrimp recaptured during successiv time increments within each experiment suggeste that von Bertalanffy's (1938) growth-in-weigh equation offered, as it has in a wide variety c species, the most meaningful and at the sam time the most practical solution to the probler of mathematically characterizing shrimp growt (fig. 9). In addition to the exponent b, which i obtained from the weight-length relationship, th function itself,

$$w_t=W_\infty(1-e^{-K(t-t_0')})^b,$$

contains three parameters that are presume effectively constant when describing growth ove the greater part of the shrimp's life span. W represents the asymptotic or maximum weigh attained by the average shrimp; K is a coefficien proportional to the rate of catabolism; and t defines a hypothetical age at which the shrimp' weight would have been zero had its growth pattern always been the same as that suggested by the experimental data.[5] If growth be assume isometric, then b takes the value 3; in the presen case, the estimated value, 3.14, was employed For more extensive discussions on the rationale underlying the von Bertalanffy equation and the advantages that render it particularly adaptabl

Table 5.—*Mean lengths and weights of marked pink shrimp recaptured during successive 4-week periods of the Sanibe experiment, December 1960–June 1961 (sexes combined)*

Month of experiment t_i	Number recaptured n	Distribution of males	Mean length l	Mean weight w	Range in weight	Equivalen number per pound (headless)
		Percent	*Mm.*	*G.*	*G.*	
0	[1] 463	46	75.3	3.5	1.8– 8.9	20
1	[2] 1	0	111.7	12.1	----------	5
2	4	100	109.1	11.0	8.2–13.8	6
3	39	38	117.5	14.1	7.1–24.8	5
4	65	52	123.0	16.3	8.1–29.5	4
5	38	39	136.1	22.5	14.4–40.2	3
6	6	33	145.8	27.7	21.9–32.5	2
7	[2] 1	0	157.5	35.2	----------	2

[1] Indicates number of specimens sampled to determine mean length anc weight of marked shrimp at start of experiment.

[2] Data from single recaptures not used in growth computation. One additional specimen (♂) recaptured in 12th month was also disregarded.

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[5] To remind the reader that the estimation of growth parameters from mark recapture experiments necessarily involves the translocation of size and time axes, the notation t_0' herein replaces the standard t_0'. The latter represent the true population parameter which may be most accurately estimated only when a reasonably complete series of weight-at-age data for a given species is available. For all practical purposes, it is assumed that the difference between t_0' and t_0', or bias, is negligible.

Throughout this paper, the symbols e and ln designate, respectively, the base of, and abbreviation for, the natural or Naperian logarithm.

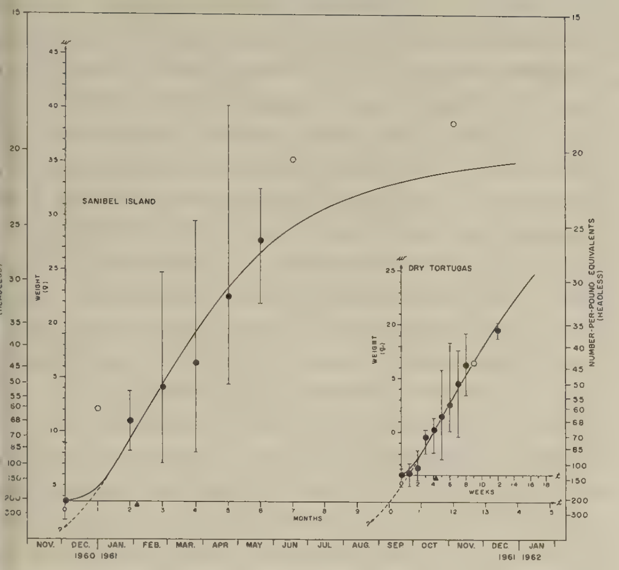

FIGURE 9.—Growth in weight of pink shrimp. Curves are fitted to mean weights of marked shrimp recaptured during successive time intervals of the Tortugas and Sanibel experiments (sexes combined). [Open circles indicate weights of single recaptures not used to fit curves.]

to incorporation in theoretical population models, the reader is referred to the works of von Bertaanffy (1957), Beverton and Holt (1957), Ricker (1958), and Tomlinson and Abramson (1961).

Approximations to W_∞ were obtained by first transforming the von Bertalanffy equation to a form linear in $w_t^{1/b}$ and then fitting the linear regression of $w_{t+1}^{1/b}$ on $w_t^{1/b}$. The intersection of the resulting line with that of proportionality yielded, upon retransformation, the desired estimates (Beverton and Holt, 1957, p. 283). In effect, the intersect signifies the approximate weight at which the ratio of successive growth increments reaches unity, i.e., growth is arrested and maximum weight is attained. The slope of the regression line provides an estimate of e^{-K}.

A distinct disadvantage of this method when working with data from mark-recapture experiments is the requirement that weights be obtained for every one of a reasonably wide range of successive, equal-width time intervals. Unfortunately, W_∞ is quite sensitive to changes in the slope of the fitted line and therefore has real meaning only when the marked population that yielded the data was at all times completely vulnerable to the sampling (fishing) gear, the sex ratio of recaptures remained static, and the resulting mean sample weights display consistent as well as good reliability. Thus, its estimation from the somewhat inadequate Sanibel data had to rely on but four pairs of values (from t_2-t_6), whereas that from the superior Tortugas data was substantiated by seven pairs (from t_1-t_8). Because of considerably less variation about the fitted line, the estimate derived from the Tortugas data is regarded the more stable, and hence the more meaningful of the two (table 6). When estimating W_∞, there was no suggestion in the case of the Tortugas data, and only faint evidence in the Sanibel data, that the fishing gear in general use was selective for faster-growing individuals during the early stages of either experiment.

TABLE 6.—*Pink shrimp growth statistics computed from mean weights of marked shrimp recaptured during successive time intervals of the Tortugas and Sanibel experiments (sexes combined)*

Experiment	Season	Duration	Width of experimental time interval, t	W_∞	K	t_0'
		Weeks	*Weeks*	*G.*		*Weeks*
Tortugas	Sept.-Dec.	12	1	[1] 42.0	0.071	0.68
Sanibel	Dec.-June	32	4	35.6	0.339	3.20

[1] Equivalent to a size of 17 headless-count.

After adjusting w_t and W_∞ to unity at the beginning (t_0) of each series of data, the slope of the linear relationship

$$\ln\left(W_\infty^{1/b}-w_t^{1/b}\right)=\{\ln\left(W_\infty^{1/b}\right)+Kt_0'\}-Kt$$

provided estimates of K, and the ordinate at which the regression line intersects $\ln W_\infty^{1/b}$ gave estimates of t_0' (table 6). Substituting these in the von Bertalanffy equation, theoretical values for w_t were calculated and ultimately defined the curves depicted in figure 9. It is assumed that the values for the constant t_0', although based on data of weight at undetermined age, would have compared reasonably well with those obtained had the actual (rather than the relative) age at each t_i been known.

From table 6 and figure 9, it may be concluded that the results of both experiments are in large degree mutually corroborative. With the Tortugas results arbitrarily established (on statistical grounds) as the standard for comparison, W_∞ is of the same relative order of magnitude while the growth indices, K, agree surprisingly well (comparative K from the Sanibel experiment=0.339/4=0.085). Weekly growth during the Tortugas experiment averaged roughly 1.5 g. in terms of weight and about 3.4 mm. in terms of total length. From a commercial fisherman's viewpoint, the experimental data (table 4) reveal that it took 12 weeks for the average shrimp to increase in size from 123 to 37 count (headless). Observe also that the minimum commercial size (70 headless-count) in the marked populations was attained about 9 weeks following the start of the Sanibel experiment, and 4½ weeks after the Tortugas experiment began.

AGE AT RECRUITMENT—MAXIMUM AGE

If, as Beverton and Holt (1957) argue, biological rather than mere empirical significance be attached to von Bertalanffy's equation and, further, if the growth pattern as fixed by the constants computed earlier be assumed reasonably typical of pre- as well as postrecruit development, then extrapolation of the curves in figure 9 to the left of t_0 should provide a rough index to the actual ("average") age of shrimp making up each experimental population at the time it was established. Adding this to the time lapsing between an experiment's initiation and the attainment of minimum commercial size by its elements gives a measure of age at recruitment. Fear that the von Bertalanffy equation may not adequately describe growth during the shrimp's earliest developmental stages should not deter pursuit of such an index. No better approach to solving the vexatious problem of age determination in commercial Penaeidae has yet been developed.

In treating accordingly the results of the Tortugas experiment (upon which all subsequent analyses and discussions will be based), a value between 10 and 11 weeks was indicated as the probable age of shrimp released at the experiment's start. When this value is extended by the 4½ weeks the marked shrimp required to reach minimum commercial size, an approximation of 15 weeks for their age at recruitment is obtained. Despite the likelihood that this value may not be too precise, its order of magnitude is quite reasonable in view of what has been observed in a species closely related to (and often occurring with) the pink shrimp, viz., the brown shrimp.

Along the Texas-Louisiana Gulf coast and with little year-to-year variation in chronology, heightened spawning activity in offshore brown shrimp populations during February and March normally results in large masses of postlarvae entering adjacent estuaries during mid-March to mid-April. Present studies by personnel at the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Tex., are yielding good evidence that brown shrimp postlarvae, 8 to 1 mm. long when they reach the barrier island passes, are on the order of 3 to 4 weeks old.[6] Once in inshore waters they grow very rapidly and begin their seaward migration about mid-June as subadults of a size just below the 70-count minimum established above. Thus, the total lapse in time between hatching and attainment of 70-count size (about 10.5 g.) is roughly 15 weeks, which agrees very well with the value obtained for pink shrimp from the Tortugas experiment.

One other growth-associated feature of pink shrimp life history about which the yield equation employed in a later section requires information is the maximum age, on the average, that this species attains. For the common Penaeidae, it has been generally assumed on empirical grounds that 18 months (78 weeks) is a good approximation thereto (Kutkuhn, 1962). Recent analyses of weight frequency distributions in commercial pink shrimp landings indicate, however, that the lapse between an age group's recruitment and its disappearance from the fishery (i.e., its fishable life span) averages about 68 weeks (Kutkuhn, 1962). Hence, upon combining this value with that of the species' average age at recruitment calculated above, a value of 83 weeks, believed to be a better estimate of maximum age, is obtained.

ESTIMATION OF MORTALITY

BASIC ASSUMPTIONS

Computationally as well as conceptually, measurement of mortality—especially natural mortality—is without question more intractable than that of growth and therefore makes greater demands on experimental data. Moreover, since the investigator cannot guarantee that the results of even the most carefully executed mark-recapture experiment will satisfy all theoretical requirements, ne is forced when attempting such measurement to rely heavily upon certain conditional assumptions that may or may not be warranted.

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[6] Lindner and Anderson (1956) offer supporting documentation in their study of the contemporary white shrimp, *P. setiferus*, whose postlarvae are also estimated to be about the same age when they enter estuaries at comparable sizes.

Potential sources of bias affecting the accuracy of mortality estimates anticipated from data yielded by the Tortugas experiment have already been discussed. To reiterate, assumptions for which reasonable substantiation was given are: (1) No, or only negligible, losses of experimental shrimp due to rough treatment at release, or to predation during and immediately after release; (2) no losses attributable at any time to aftereffects of the mark (dye); (3) little if any movement of marked shrimp from the range of effective fishing during the experiment; and (4) negligible loss of recaptured shrimp because of failure to report them. Information indicating the percentage loss due to nondetection was not obtained, but the manner in which commercial catches were processed leaves little doubt that the likelihood of detecting marked shrimp was high (as was the incentive to do so). Nevertheless, a necessary assumption is that not only was the number of recaptured but undetected shrimp low, but that the ratio of undetected to detected recaptures did not change during the experiment.

THEORY AND EXPERIMENTAL RESULTS

All present-day theory constituting the framework of what is commonly termed "population dynamics" has as its point of departure the concept that the average rate of decline in any population (fish, shellfish, etc.) is at every instant proportional to population size. This relationship may be simply expressed by the differential equation

$$\frac{dN}{dt}=-ZN$$

which, upon integration, gives the geometric progression

$$N_t=N_0e^{-Zt} \qquad (1)$$

with common ratio e^{-Z}, N_0 the initial population size, and N_t the number in the population during any of a series of equal-width time intervals t. Two parameters, N_0 and Z, characterize the expression, with the coefficient Z referred to as the instantaneous rate of total mortality.

The foregoing theorem proves particularly useful in mark-recapture work since the initial size of a marked population, N_0, is almost always known. In some situations this feature readily permits the separation of Z into its components, viz., (1) mortality in the experimental population due to recapture (fishing), and (2) losses of marked members due to all other causes. These quantities are symbolized in the following analysis by the notation F and X, respectively (Beverton and Holt, 1957). Of major interest is the coefficient X, part of which represents true natural mortality, hereinafter denoted by the symbol M. Depending on the acceptability of assumptions concerning the degree to which marked members are not prone to loss other than through fishing and natural mortality, X itself can provide a reasonable approximation of M.

As revealed earlier (fig. 5), the probability of a marked shrimp being recaptured varied widely during the Tortugas experiment. It follows that the corresponding fishing mortality fluctuated accordingly, and that the effects of nonuniform recapture effort would therefore have to be eliminated before attempting to measure total mortality, Z, and, ultimately, natural mortality, M. Two approaches to the satisfactory measurement of Z with recapture data generated under such circumstances are employed herein, whereas only a single alternative offered itself as a solution to the more difficult problem of estimating X (i.e., M).

The first of the two methods used to determine Z entailed application of an analytical method developed for the simple situation where fishing effort (or intensity) does not change appreciably during an experiment. Its use here initially required that, rather than assume within each equal-width time interval a fixed but, between intervals, a successively different (i.e., a discontinuous) fishing mortality, the number of recaptures accumulating in every time interval be adjusted to a continuously uniform fishing effort throughout the experiment (table 7). Such an approach clearly infers that had a static fishing effort prevailed, the pattern of population decline expressed by theorem (1)—with all bias constant or negligible—would have been reflected. In other words, removing the confounding effects of a varying fishing effort served to eliminate all but that part of the overall recapture probability that would have diminished predictably as the experimental population declined. It is noteworthy that adjustment of each value in the recapture time-series under discussion here was itself independent of time, and hence did not superimpose additional bias whose presence might further curtail the usefulness of mortality coefficients to be estimated by regression techniques from data already serially correlated.

Since it was derived specifically to cover the general case where fishing effort varies throughout an experiment, the second method, which yielded estimates of X as well as Z, did not necessitate any preliminary adjustment of raw data. In large degree, measurements of Z by both techniques proved mutually confirmatory.

TABLE 7.—*Unadjusted and adjusted numbers of marked pink shrimp recaptured during successive weeks of the Tortugas experiment, September–December 1961*

[Number liberated (N_0)=2,090]

Week of experiment t_i	Number recaptured n	Distribution of males	Estimated total fishing effort [1] f	Number recaptured per 1,000 hours' fishing effort n'	Log adjusted number recaptured $\ln n'$
		Percent	*Thousands of hours*		
0	47	55	2. 11±0. 23	22. 3	3. 105
1	68	51	2. 80±0. 52	24. 3	3. 190
2	44	54	3. 98±0. 30	11. 1	2. 407
3	15	47	2. 82±0. 30	5. 3	1. 670
4	14	61	0. 92±0. 11	15. 2	2. 721
5	184	55	3. 78±0. 20	48. 7	3. 886
6	37	42	4. 04±0. 43	9. 2	2. 219
7	24	67	5. 83±0. 47	4. 1	1. 411
8	6	67	10. 07±0. 62	0. 6	−0. 511
9	1	100	5. 43±0. 43	0. 2	−1. 609
10	0	----------	6. 98±0. 73	0. 0	----------
11	0	----------	8. 92±0. 65	0. 0	----------
12	3	33	9. 14±0. 48	0. 3	−1. 204

[1] 0.80 confidence intervals.

Subdivision of the Experiment

Preparatory to mortality estimation, plots of the adjusted Tortugas recapture data revealed a distinct but not unexpected discontinuity in the pattern of exploitation during the experiment (fig. 10). Prior to its fifth week, in which most members reached a size acknowledged to be the commercial minimum, the experimental population experienced a measurable amount of purposively selective fishing. Not until the beginning of the experiment's sixth week can it be presumed that recruitment to the "commercial" population was effectively complete. Most interest attaches to the experiment's second phase since estimates of fishing mortality between the points of complete recruitment to and virtual disappearance of the marked population from the fishery (i.e., fro t_5 to t_{10}), and natural mortality just prior to an over the same period (i.e., from t_4 to t_{10}), ar included among the major objectives of thi study.

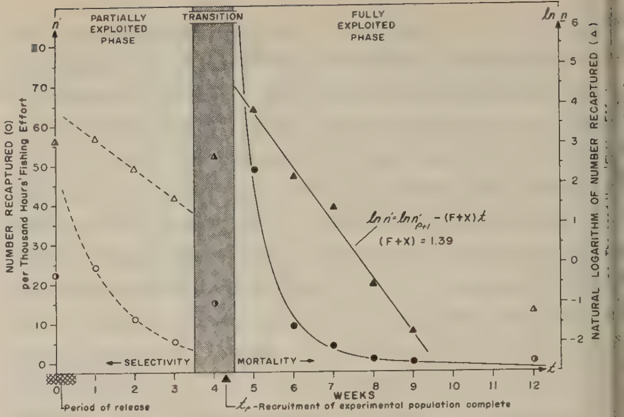

FIGURE 10.—Mortality of pink shrimp. Curves are fitte to numbers of marked shrimp recaptured during successive weeks of the Tortugas experiment (September December 1961) and adjusted for nonuniform fishin effort. [Number liberated (N_0)=2,090.]

The experiment may therefore be conveniently subdivided into two phases arbitrarily separated by a brief (1-week) interval of transition. They are: (1) A period in population development when the fishery exercised moderate selectivity—the partially exploited phase, which was characterized by varying degrees of purposive as well as gear selectivity; and (2) a period of nonselectivity—the fully exploited phase, during which every population member was vulnerable to all operating causes of mortality.

Total Mortality During Partially Exploited Phase

Proceeding from theorem (1), which, upon transformation to logarithmic form, becomes linear in $\ln N_t$ and t, Beverton and Holt (1957, pp. 185–191) give in terms of the recaptures themselves a comparable expression intended for use with marked populations subjected to a uniform fishing (recapture) effort. Thus, making appropriate substitutions,

$$\frac{dn}{dt} = FN_t = FN_0e^{-(F+X)t}$$

and, ultimately,

$$\ln n_2 = \ln n_1 - (F+X)\tau \qquad (2)$$

where $n_1, n_2, \ldots n_i$ refer to the number of marked individuals recaptured during the first, second, . . . i^{th} time interval t, respectively; $\tau = t_{i+1} - t_i$ $(=1$ week); F and X are the instantaneous coefficients of reduction of marks due, respectively, to fishing and to all causes other than fishing; and $(F+X)=Z$. It follows from expression (2) that a linear regression of the natural logarithms of successive numbers of recaptures on time gives estimates of $\ln n_1$ and Z.

Fitting a regression to the logarithms of Tortugas recaptures grouped by weeks and adjusted for nonuniform fishing effort (viz., $\ln n_1'$ through $\ln n_3'$, where the prime indicates an adjusted value) yielded an estimate of 0.76 for Z, the only parameter of interest during the experiment's initial phase. Figure 10 shows that the regression enjoyed a good fit.

Obviously, a measurable amount of (selective) fishing effort contributed to the total mortality value so obtained, though by far the greater share of this value is presumed attributable to natural causes. Only a very minor part is believed due to the "other-loss" factors defined earlier. There is moreover, no statistical evidence of any differential vulnerability of sexes during the partially exploited phase. Despite the slower growth noted for males, the sex ratio of recaptures never departed significantly from that observed at the start of the experiment (table 7). In summary, a small amount of fishing activity during the experiment's first phase was sufficient to demonstrate an apparently high corresponding rate of natural mortality, which, as will be shown later, continued well into the second or fully exploited phase. Here it became associated with the relatively high rate of fishing mortality established at the moment recruitment was completed.

Mortality During Fully Exploited Phase

After plotting the logarithms of the adjusted numbers of shrimp recaptured during the first 5 weeks of the Tortugas experiment's fully exploited phase, and observing that they, too, all fell nearly in a straight line (fig. 10), computation of their linear regression on time [equation (2)] gave a first estimate of $Z=1.39$ for the instantaneous coefficient of mark reduction due to all causes.

Attempts to subdivide the resulting Z into its fishing mortality and "other-loss" components proved impractical, however, when recapture data adjusted for varying fishing effort were substituted in techniques implicitly designed for unadjusted data generated by a uniform effort. Inspection of the basic equations involved (Beverton and Holt, 1957, p. 190, equations 14.15 and 14.16) reveals that the soundness of F and X (or M) estimated therewith may be influenced not only by the size of N_0 (or any specified equivalent), but also by variation in the relative magnitude of the antilog of $\ln n_1$ (or its counterpart), where the latter value is derived by means analogous to equation (2). It will be recalled that initial treatment of the recapture data entailed their being grouped on a weekly basis, and then adjusted within each time unit for nonuniformity of fishing effort between units by a factor equal to the reciprocal of the quantity $(f_i \times 10^{-3})$, with f_i representing the overall effort in hours expended on the fishing grounds during the i^{th} weekly interval (table 7). Subsequent difficulty stems from the arbitrary nature of the attenuation index, 10^{-3}, which must be selected so as to yield adjusted recapture values having an average order of magnitude moderately close to that of the unadjusted values.

Whereas analysis of recapture data so adjusted provides [through expression (2)] a good estimate of the total-loss coefficient $Z=(F+X)$, such subjective treatment imparts bias of unknown degree to the values for F and X when these are delineated by the equations mentioned above. This bias will be proportional to the value of n_1 as estimated by expression (2), and, accordingly, to the relative size of the adjustment index employed. The real problem, however, lies in not being able to specify satisfactorily the relationship between N_0 and the estimated initial value of the recapture time-series based upon adjusted data, as contrasted to that between N_0 and the corresponding value of the time-series involving unadjusted data.

Drawing support from the fundamental theorem stating that over a given time interval r, fishing mortality is proportional to fishing effort (or intensity), i.e., $F_r = cf_r$, Beverton and Holt (1957, p. 192) derive solely in terms of recapture and related effort values a useful equation which furnishes—independent of N_0—an estimate of the other-loss coefficient X, regarded herein for the reasons outlined earlier as a close approxima-

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tion of M. This equation is given by

$$\frac{1}{\tau_r}\left[\ln\left(\frac{n_r f_{r+1}}{n_{r+1} f_r}\right) + \ln\left\{\frac{(cf_r+X)(1-e^{-(cf_{r+1}+X)\tau_{r+1}})}{(cf_{r+1}+X)(1-e^{-(cf_r+X)\tau_r})}\right\}\right] = cf_r+X \quad (3)$$

where τ signifies the width (in weekly units) of experimental time intervals r or $r+1$, n identifies the number of recaptures in the same intervals, and c denotes the average coefficient of proportionality relating fishing mortality to fishing effort, f_r.

Equation (3), accounting inherently for varying fishing effort, is linear in f_r and a logarithmic expression (left side) corresponding to the ratios in successive time intervals of the numerical abundance of marked individuals composing the experimental population. Accordingly, simple regression procedures involving at least two iterations lead to fairly good estimates of c and X, the slope and y-intercept, respectively. The latter value may be viewed as a measure of the average total-loss rate that would have prevailed during the experiment in the absence of any fishing activity.

Use of expression (3) assumes that bias introduced by the practical need to treat fishing effort as a discontinuous function of time is negligible. Its application to appropriate recapture data and corresponding values of effective fishing effort gave, after three iterations, estimates of $c=0.171$, $X=0.55$, and average $F=0.96$ for the fully exploited phase of the Tortugas experiment (fig. 11). Interestingly, the resulting value for $Z=(F+X)=1.51$ compared quite favorably with the preliminary value calculated earlier, viz, $Z=1.39$, differing on the order of but 9 percent. Relevant statistics are presented in table 8. Note here the incorporation of effort data slightly modified from those used earlier to obtain the preliminary estimate of Z. The decision to subject to analysis only those measurements of effort expended inside 20 fathoms was prompted by the observation that none of the 252 marked shrimp retrieved during the period of interest (table 8) was recaptured beyond this range. Such adjustment seemed necessary to minimized the likelihood of violating, in terms of the experimental population and that portion of the fishery's overall activity directly associated with it both spatially and temporally, the functional relationship between fishing mortality and fishing effort (or intensity) stated above.

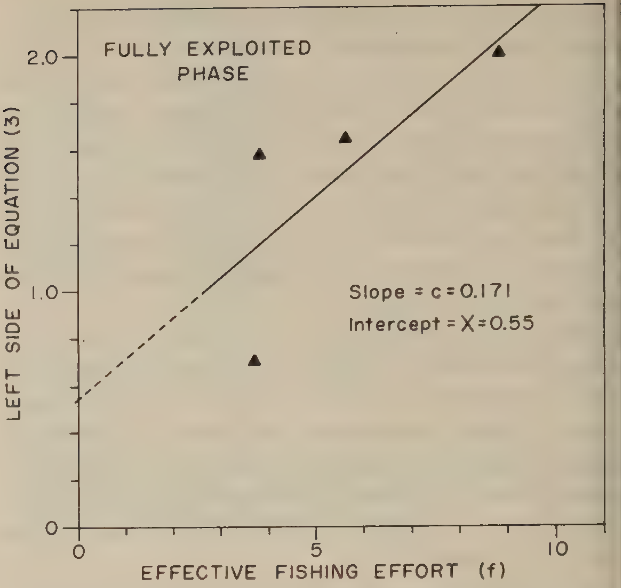

FIGURE 11.—Estimating the other-loss coefficient X using equation (3) of text. [Refer to table 8 for description of data and associated statistics.]

Transformation of estimated F and X to corresponding weekly rates of reduction in marks resulted in values of 0.62 for that due to fishing, and 0.42 for that due to all other causes (see Ricker, 1958, p. 25, for discussion of relationships). These results, while indicative of greater mortality pressure on parent shrimp populations than had

TABLE 8.—*Statistics employed to estimate with equation (3) of text the other-loss coefficient X for the fully exploited phase of the Tortugas experiment*

[Resulting F values are given in the last column; c=0.171]

Week of experiment t_i	Rank in time-series r	Width of experimental time interval	Number recaptured n	Estimated effective fishing effort [1] f	Left side of equation (3)	Estimated fishing mortality $F=cf$
		Weeks		*Thousands of hours*	*Ln units*	
5	1	1	184	3.78	1.583	0.65
6	2	1	37	3.68	0.725	0.63
7	3	1	24	5.60	1.642	0.96
8	4	1	6	8.76	1.996	1.50
9–10	5	2	1	11.73	----------	2.01

[1] Treated here as synonymous with *fishing intensity* which, in broader geographical application than is here necessary, is explicitly defined as fishing effort per unit area; data represent only that amount of effort expended on the Tortugas fishing grounds inside the 20-fathom contour (re table 2).

been widely spectulated, are not unreasonable when one considers the species' high reproductive potential, short life expectancy, gregarious habits, and, presumably, its sensitivity to environmental fluctuations. Such characteristics, as they control population development, are not atypical of Arthropoda in general.

Returning to the matter of discontinuity in temporal distribution of recaptures during the Tortugas experiment (table 7, fig. 10), observe now that its further reconciliation is possible. The value obtained for X, 0.55, which is henceforth assumed for the reasons noted earlier to have been practically all due to natural causes, is readily contained in the total-loss coefficients estimated for both partially and fully exploited phases, viz, 0.76 and 1.51, respectively. If natural mortality is presumed to have been effectively constant through the transition period, then the difference in residuals (fishing mortalities, $F=0.21$ versus $F=0.96$) may be immediately attributed to cessation of selective fishing accompanied by an abrupt rise in fishing rate upon completion of recruitment. It appears that had the low rate of recapture established during the partially exploited phase continued, subsequent computations would also have led to an estimate for X (hence M) comparable to that determined from existing data for the fully exploited phase.

That the instantaneous rates of mortality do not remain constant over extended periods of time but diminish with age is suggested by a small number of marked shrimp having been recaptured late in the experiment. Note in figure 10 that their corresponding logarithm fell far to the right of the line fitted to those of adjusted numbers of recaptures made earlier in the experiment.

In summary, the foregoing results are interpreted to reflect exclusively conditions in that age group of shrimp represented by the experimental population, and hence should only be applied with great caution in other fisheries, or to other age groups at different seasons. Every age group (as herein defined) is but one of a succession of groups that may overlap several seasons. Each is therefore likely to be subjected at every stage of development to different levels of exploitation as well as to changing ecological conditions, with the high expectation that mortality parameters will vary accordingly.

YIELD IN WEIGHT AS A FUNCTION OF AGE (SIZE) AT RECRUITMENT

To answer the fundamental question posed earlier, it remains now to express the interaction of population growth and mortality in terms of expected yield when age (or size) at recruitment is varied over a wide range of values. Thus, so that the commercial return from a particular age group (or, in general, all age groups combined) will be maximal, at what average age of shrimp, under the conditions of observed growth and mortality, should harvesting begin?

THEORETICAL POPULATION MODEL

A satisfactory answer may be provided through application of any one of several mathematical population models, or analogs, which have been developed to facilitate study of the dynamics of open, self-maintaining biological systems (e.g., Watt, 1956; Beverton and Holt, 1957; Ricker, 1958). Notwithstanding its possible shortcomings, all of which are thoroughly discussed at appropriate stages in its derivation, the simple model developed and applied by Beverton and Holt (1957, pp. 35–38 and 309–327) was chosen for the purposes of this study because it offered the most straightforward solution to a practical problem.

Deterministic in nature, i.e., growth and mortality are presumed effectively constant from recruitment onward to the end of the species fishable life span, the expression for the shrimp population's mean weekly biomass over this period is given by

$$\bar{P}'_W = Re^{-M\rho} W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK} \left(1-e^{-(F+M+nK)\lambda}\right)$$

where F and M are, respectively, the coefficients of instantaneous fishing and natural mortality; W_∞, K, and t_0' are the growth parameters defined earlier; R represents the number of shrimp recruited weekly to the fished population; $t_{\rho'}$ is the age, corresponding to the minimum commercial size referred to above, at which recruitment is no longer influenced by selective fishing; $\lambda=t_\lambda-t_{\rho'}$ indicates the population's fishable life span (t_λ being the species mean life expectancy); and $\rho=t_{\rho'}-t_\rho$ designates an interval during which some recruitment occurs because of selective fishing but population decline is mainly attributable to natural causes (t_ρ indicating the age at which shrimp become liable to selective capture but, generally speaking, have not yet attained commercial acceptability). In practice, for a given set of conditions, ρ is usually negligible and $t_{\rho'}$ and t_ρ may be considered equivalent. The remaining notation arises from the need, during the model's development, to expand the exponential term of the von Bertalanffy growth equation.

Thus, if we let $b=3$,

$$w_t=W_\infty(1-e^{-K(t-t_0')})^b$$

may be algebraically transformed to

$$w_t=W_\infty\sum_{n=0}^{3}\Omega_n e^{-nK(t-t_0')}$$

where the appropriate coefficients of the binomial expansion are

$$\Omega_0=+1,\ \Omega_1=-3,\ \Omega_2=+3,\ \Omega_3=-1$$

with n taking the values 0, 1, 2, and 3. Although earlier analysis of the weight-length relationship suggested that growth in pink shrimp is not truly isometric, use of the foregoing model assumes, for practical purposes, that it is. Actually, the minor effects of a departure from isometry should be taken into account by appropriately varying W_∞, but failure to do so here does not lessen the validity of later findings.

From the biomass equation just postulated, it follows that an expression for the mean weekly yield of the fished population may be represented by

$$Y_W=F\bar{P}_W'.$$

And since R, the recruitment, is the only one of the parameters describing $\bar{P}_W'$ that is not ordinarily amenable to measurement, further modification results in

$$\frac{Y_W}{R}=\frac{F\bar{P}_W'}{R}=Fe^{-M\rho}W_\infty\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0')}}{F+M+nK}(1-e^{-(F+M+nK)\lambda}) \quad (4)$$

hereinafter referred to as the expected yield in weight per recruit.

DETERMINATION OF YIELD MAXIMUMS

By varying $t_{\rho'}$, and hence ρ and λ, curves of yield as a function of age can be generated with equation (4) for fixed values of the remaining parameters. The process obviously entails prior establishment of some absolute minimum value for t_ρ, this value corresponding in subsequent analyses to a size below which all shrimp are not only commercially unacceptable, but also incompletely vulnerable to the gear in common use.

Yield Curve for Observed Parameter Values

We have, from the Tortugas experiment and other sources, the following values for the indicated parameters:

$$M=0.55 \qquad t_0'=0.68 \text{ week}$$

$$F=0.96 \qquad t_\lambda=83 \text{ weeks}$$

$$K=0.07 \qquad t_\rho=15 \text{ weeks}^{7}$$

$$W_\infty=42.0 \text{ g.}$$

Recall also that $\lambda=t_\lambda-t_{\rho'}$ and $\rho=t_{\rho'}-t_\rho$. Substituting these in equation (4) and solving it for each of not less than nine carefully spaced values of $t_{\rho'}$, the yield curve farthest to the left in figure 12 was obtained. It is immediately apparent from this figure that in a population whose development is governed by growth and natural mortality of the magnitude observed for the Tortugas pink shrimp population, peak biomass is attained somewhat before, rather than after, the average shrimp reaches a size equivalent to the present commercial minimum. Growth, although relatively high in contrast to that determined for a variety of species supporting other commercial fisheries, evidently cannot compensate (to man's economic advantage) for losses accruing to a high natural mortality. Nor is postponement of full-scale exploitation indicated unless reduced environmental effects can be expected to result in a markedly lower natural mortality. Under observed conditions, delaying exploitation until the shrimp reach a greater initial size would indeed result in a negligible gain in yields of so-called premium shrimp, but only at the expense of a significant reduction in the total yield of all sizes.

Yield Curves Theorizing Lower Levels of Natural Mortality

Of the parameter estimates obtained in this study, by far the firmer and at the same time the least subject to wide temporal variation are those

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[7] Age roughly corresponding to the minimum commercial size of 70 headless-count.

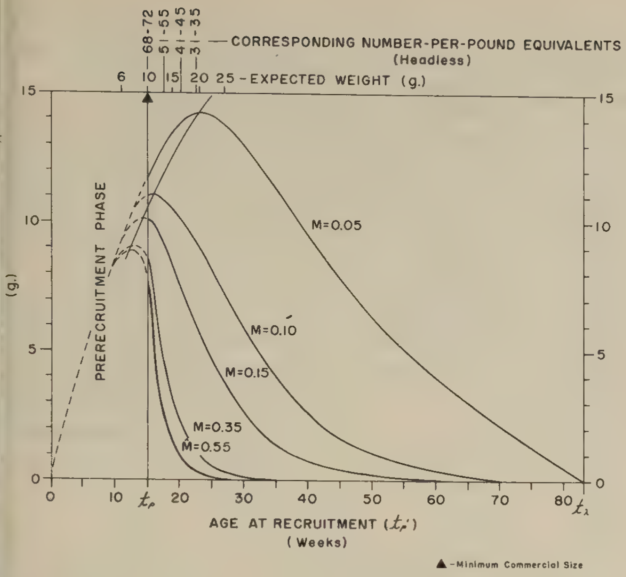

FIGURE 12.—Yield in weight per recruit against age at recruitment for different levels of natural mortality (M) in a population of pink shrimp. [F=0; 96, K=0.07; W_∞=42.0 g.; ^ indicates an observed as contrasted to a hypothetical value.]

describing growth. In contrast, greater variation would be expected for natural mortality since it may be readily conceived ,as the more sensitive to and hence the more likely of the density-dependent parameters to reflect even the most subtle of environmental vagaries. In other words the potentialities for growth in the individual are largely predetermined within rather narrow limits by the characteristics of the species; those for natural mortality, which are enhanced through great prolificness, largely by the environment.

With this in mind, additional curves were generated in like manner for four hypothetical and successively lower values of the natural mortality coefficient (fig. 12). These illustrate very clearly what happens when, with respect to some economic standard t_p, natural mortality becomes increasingly compatible with growth. For any magnitude of exploitation (F), maximum yields will always occur at higher levels and at more advanced recruitment ages as natural mortality establishes itself at lower and lower levels. Under the growth restrictions imposed here, postponing initiation of exploitation would not be justified unless the observed natural mortality rate were on the order of 0.10 or less. It may be argued now that even if the observed value for M (0.55) constituted a gross overestimate of the true natural mortality, the associated error would have had to be rather large before the general conclusion just reached could be viewed with suspicion. The present example also shows that with a natural mortality of 0.05 (which is untenably low for shrimp), the highest yield is obtained when age at recruitment is increased to about 23 weeks, this corresponding to a shrimp size of roughly 31–35, headless-count. Dashed portions to the left of t_p arbitrarily designate the likely order and shape of the yield curves for that part of the hypothetical population not yet possessing economic worth.

Effects of Variation in Rates of Growth and Exploitation

To illustrate how changes in the critical factors of growth and fishing mortality influence the yield curve's shape and the position of its maximum point, curves for selected (hypothetical) parameter values are compared with those derived above for observed values. If yield is described as a function of age at recruitment for varying rates of growth (fig. 13A), it will be noted that the effect of a higher rate of growth than that observed is an increase in amplitude of the yield curve and a shift in its maximum point to the left, with whatever recruitment size is designated as the standard minimum remaining the same as before. In other words, every shrimp reaches the smallest acceptable size at an earlier age. Conversely, at a given level of natural mortality, a lower rate of growth tends to decrease curve amplitude and move the point of maximum yield to the right, the minimum marketable size again remaining fixed but being attained at a later age.

Exercising care to judge each new set of conditions on its own merits, it appears that increased rates of growth such as postulated in figure 13A would still not be sufficient to justify any advance of recruitment age where a high natural mortality prevails. At a low mortality level, an advance of recruitment age is indicated only when concurrent growth is also of a low order. Hence, for a fixed natural mortality, successively higher rates of growth would merely dictate a retrogression in recruitment age (but not size) if maximum yield is to be achieved. This relationship implies no change in minimum acceptable size at recruitment but, instead, as in the observed situation where low growth rate complements high natural mortality, a greater overall yield by the age group involved during its fishable life span.

By comparison, changes in the level of fishing may be expected to produce only relatively minor differences in both the position and height of yield curve maximums (fig. 13B). The revelation that the magnitude of fishing (F) is actually of little concern when deciding at what age or size to begin harvesting a resource in order to achieve maximum yields should not create the impression that fishing mortality has no significance at all. Although maximum utilization of a domestic shrimp resource is the issue under discussion here, the fact remains that resource maintenance is still the overriding objective of shrimp research. As pointed out earlier, the matter of recruitment age or size is at this point largely one of economics. Yet to be answered is the question of how much (in contrast to what size) shrimp may be harvested and still have sufficient residual to maintain the resource at the highest level consistent with projected environmental conditions. In effect, rather than inquiring as to the optimum $t_{\rho'}$, we should perhaps be asking: What is the optimum F?

Employing commercial fishery statistics, a prior analysis of the Tortugas pink shrimp stock gave rise to speculation that a decline in production over the period 1956–59 was attributable more to poor utilization of supplies than to too intensive fishing and hence improper maintenance of the stock (Kutkuhn, 1962). The observation was made that increasingly heavy exploitation of new recruits, as they enter the fishing grounds and before their average growth rate reaches a maximum, appeared to have systematically reduced annual biomass. Although this conclusion seems to be in conflict with the findings of the present study, it must be stressed that the earlier analysis was necessarily cursory due to certain data inadequacies and that it attempted to generalize over a long period of time and a variety of conditions. In contrast, the results reported here represent a well-organized effort to acquire the information needed to answer specifically the question posed. They are therefore quite explicit where the others were not, and, accordingly, merit much greater attention and could even be put to interim use.

The present findings do not, however, constitute the final solution to the stated question. As did those of the first analysis, they only reflect the accumulation of more and better data, and merely serve as one of several anticipated stepping stones toward an unassailable objective.

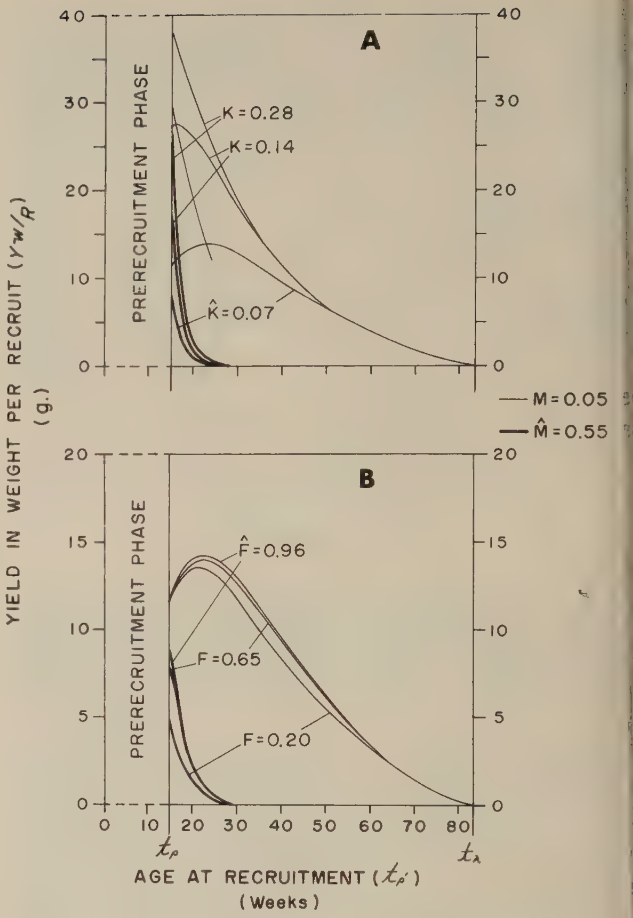

FIGURE 13.—Yield in weight per recruit against age at recruitment for observed and hypothetical levels of growth (K), fishing mortality (F), and natural mortality (M) in a population of pink shrimp. [In plate A, $F=0.96$, $W_\infty=42.0$ g., and the ordinate through $t_\rho=15$ weeks refers, in terms of corresponding shrimp size, only to the curves for $K=0.07$; in plate B, $K=0.07$ and $W_\infty=42.0$ g.; ∧ indicates an observed value.]

YIELD IN VALUE AS A FUNCTION OF AGE (SIZE) AT RECRUITMENT

Perhaps more meaningful to the entrepreneur is an indication of the size at which harvesting should commence so that total shrimp production will enjoy highest possible value. Necessitated by consumer demands, a well-known characteristic of the Gulf coast shrimp industry is the gradation of ex-vessel price according to the size of shrimp landed and sold. Knowledge of the price-size relationship may be used to advantage in determining where, in different growth and mortality situations, the curve of yield value on recruitment age reaches a maximum.

VALUE IN RELATION TO SIZE

For the purposes of this study, particular attention was given the price structure for pink shrimp landed at Key West, Fla., during the Tortugas experiment, September to December 1961 (table 9). A plot of mean price on whole-weight equivalents for each of 11 size (headless-count) categories suggested that price could be treated as a logarithmic function of weight (fig. 14). The empirical relationship proved to be satisfactorily described by an equation of the form

$$p=a+b \ln [\ln w], \qquad w \nless 10$$

where p signifies the price per pound, w is the corresponding weight on an individual-shrimp basis, and a and b denote constants. Note that the expression has been rendered discontinuous at a shrimp weight of slightly more than 10 g., which corresponds to the minimum commercial size of 70 headless-count recognized earlier, and which commanded the lowest price then in effect (fig. 14). Dealers accepting them paid the prevailing minimum rate (30 cents per pound) for all smaller shrimp.

Having established a reasonably acceptable expression for the basic relationship between market price and individual shrimp weight, it was then possible to develop one relating the latter variable to corresponding shrimp value (fig. 14). Data generated in the process served the needs of subsequent analyses.

VALUE AS A FUNCTION OF TIME

Since shrimp value increases predictably with weight, a corollary is that it behaves similarly with respect to time. Thus, simple transformation of weight to value units results in a temporal distribution of points which may be empirically defined by the growth equation employed in a previous section. By treating the Tortugas experimental data (table 4) accordingly, estimates of the constants in the regression of value on time were computed. The counterparts of W_∞ and K, respectively, $V_\infty=4.8$ cents approximated the shrimp's maximum attainable value, and $K_v=0.08$ represented an index of the rate of value decrease; t'_0; remained fixed at 0.68 week, the value employed above in the description of growth in weight. When fitted to the experimental observations, the resulting expression for shrimp weight in terms of value as a function of time yielded a curve over the range of values 0.5 to 5.0 cents (per shrimp) closely comparable to that given by the corresponding expression for growth in weight.

DETERMINATION OF YIELD-IN-VALUE MAXIMUMS

After appropriate substitutions were made for the above growth-in-value constants, solution of equation (4) for various recruitment ages $(t_{\rho'})$ at each of four levels of natural mortality (M) permitted construction of the desired yield-in-value

TABLE 9.—*Weekly ex-vessel prices paid for pink shrimp landed at Key West, Fla., 1961*

[Values are in cents per pound for headless shrimp graded by sample (box) count] [1]

Week ending	Size category (Number per pound—headless)										
	68–72	61–67	56–60	51–55	46–50	41–45	36–40	31–35	26–30	21–25	15–20
Sept. 16	32	40	41	50	51	57	59	64	69	74	79
23	31	36	41	46	51	56	61	66	71	76	81
30	27	31	41	46	51	56	61	66	71	76	81
Oct. 7	28	34	41	46	51	56	61	66	71	76	81
14	28	34	41	46	51	56	61	66	71	76	81
21	23	29	36	41	46	51	54	61	66	71	76
28	23	29	36	41	46	51	56	61	66	71	76
Nov. 4	26	32	39	44	49	54	59	64	69	74	79
11	29	35	42	47	51	56	61	65	70	75	80
18	29	35	42	47	51	56	61	65	70	75	80
25	32	38	45	50	54	58	62	67	72	77	82
Dec. 2	32	38	45	50	54	58	62	67	72	77	82
9	32	38	45	50	54	58	62	67	72	77	82
16	32	38	45	50	54	58	62	67	72	77	82
23	32	38	45	50	54	58	62	67	72	77	82
30	34	40	47	52	56	60	64	69	74	79	84
Mean	29. 4	35. 3	42. 0	47. 3	51. 5	56. 2	60. 5	65. 5	70. 5	75. 5	80. 5
Whole-weight equivalents (g.)	10. 5	11. 4	12. 6	13. 8	15. 3	17. 0	19. 2	22. 1	26. 1	32. 5	41. 7

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[1] Source: Market News Service, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.

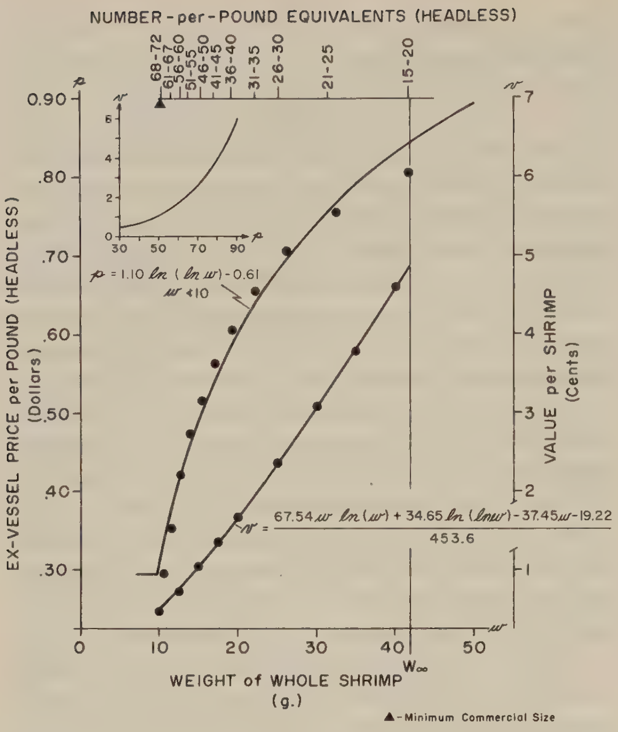

FIGURE 14.—Ex-vessel price (p) against weight (w) of pink shrimp landed at Key West, Fla., during September–December 1961. Also shown are the expression for converting price to value (v) on an individual-shrimp basis, and the resulting plot of value as a function of shrimp weight. In the upper left-hand corner, the value per shrimp in cents is graphed as a function of price per pound in the same units.

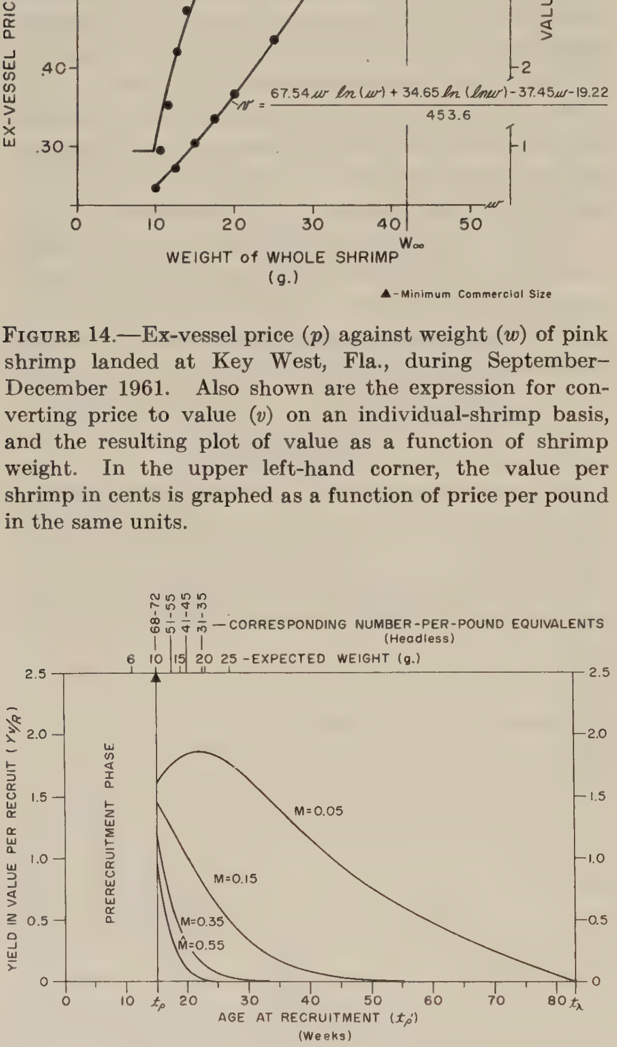

FIGURE 15.—Yield in value per recruit against age at recruitment for different levels of natural mortality in a population of pink shrimp. [F=0.96; K_v=0.08; V_∞=4.8 cents (per shrimp); ʌ indicates an observed as contrasted to a hypothetical value.]

curves (fig. 15). Upon comparing these with the yield-in-weight curves shown in figure 12, the most noticeable (though not necessarily significant) difference is seen in the relative positions of their maximum points. Unless natural mortality is extremely low, highest economic yield from a given age group during its fishable life span clearly occurs when exploitation begins as soon as the average shrimp attains commercial acceptance. In all but those circumstances where extraordinarily low natural mortality operates, no advancement of the recruitment age is indicated. This implies, of course, that the relationship between price and size holds relatively static.

Of interest is the general observation that, in situations where postponement of exploitation may be in order, maximum economic yield can be expected at a recruitment age (or size) slightly lower than that suggested for maximum biological yield. Figures 12 and 15 for M=0.05 illustrate this very nicely. Note that the yield-in-weight curve (fig. 12) reaches its highest point at a recruitment size of about 31–35 count (headless), whereas the yield-in-value maximum occurs roughly at a headless-count somewhere between 36 and 40 (fig. 15). This difference is of appreciable biological magnitude and can be largely attributed to the somewhat higher rate of growth in terms of value (K_v=0.08 versus K=0.07). To reiterate, at levels of natural mortality known to be well within the range of expectation, the total yield of a given age group during its fishable life span will be maximal only when fishing begins at the minimum marketable size. Postponement to a larger initial size would engender economic loss.

SUMMARY

Measures of growth and mortality in a population of pink shrimp obtained simultaneously by the mark-recapture technique permitted critical examination of the interrelationship of these parameters in assessing present utilization of the resource.

Of 2,090 carefully graded, precommercial-size shrimp injected with blue dye and released in late September (1961) at a point on the periphery of the well-known Tortugas (Florida) fishing grounds, 443 (21 percent) were returned during the ensuing 3 months. Recapture (commercial fishing) effort was closely surveyed throughout this experiment

and then used to remove the effects of its uneven distribution from subsequent mortality estimates. Results of an earlier mark-recapture experiment performed with the same species but in an adjacent area and for a different purpose corroborated growth-parameter estimates from the Tortugas experiment.

After the various metric relationships used to convert length to weight units were documented, the von Bertalanffy growth function was fitted to the mean weights (sexes combined) of marked shrimp recaptured during successive, equal-width time intervals characterizing each experiment. The more meticulously executed Tortugas experiment yielded for the function's parameters the values: $W_\infty=42.0$ g.; $K=0.071$; and $t_0'=0.68$ week. Weekly growth in weight during the rectilinear phase of the observed growth pattern averaged 1.5 g., which corresponded to a length increment of about 3.4 mm. In terms of commercial count size, the average experimental shrimp required 12 weeks to increase in size from 123 to 37 headless-count. Minimum commercial size (70 headless-count) was reached approximately 4½ weeks after the experiment began, and at an estimated age of 15 weeks. The life expectancy of the pink shrimp was assumed on the basis of other studies to be about 83 weeks.

The Tortugas experiment had to be subdivided into partially exploited and fully exploited phases before fishing and natural mortality could be calculated. Rates of total mark-loss during both phases were estimated by regression techniques from recapture data grouped by weeks and adjusted for nonuniform fishing effort. Separation of the value obtained for the fully exploited phase into its fishing and natural mortality components, F and M respectively, proved impractical, however, when attempts were made to apply mathematical procedures designed specifically to accommodate unadjusted recapture data generated by a constant fishing effort. Difficulty arose from an inability to evaluate satisfactorily the absolute size of the experimental population at the start of its fully exploited phase. Subsequent measurement of F and M by a procedure independent of the initial size of the marked population's second phase, and inherently accounting for varying fishing effort throughout, yielded estimates of 0.96 and 0.55 respectively. Their transformation to weekly mortality rates gave the corresponding values 0.62 and 0.42. Notwithstanding statistical limitations, these observations draw attention to the fact that at least in some areas, certain age groups (or broods) of commercial shrimp may be subjected to rather rapid deterioration from artificial as well as natural causes.

After substituting therein observed and hypothetical values for the parameters of growth and mortality, a relatively simple yield equation was solved for each in a series of selected age-at-recruitment values. With 15 weeks (corresponding to a size of 70 headless-count) established as the absolute commercial minimum age and thereby serving as the point of departure, the resulting curves of yield on age at recruitment clearly showed that unless the expected level of natural mortality falls well below that observed, postponement of fishing until shrimp reach a greater initial age (or size) is not justified. Observed growth, although comparatively high, cannot offset concurrent losses due to the substantial natural mortality that seemingly prevails when shrimp availability is at a maximum. Delaying the start of harvesting would subsequently result in slightly greater catches of shrimp in the larger size categories, but only at the expense of an appreciably diminished overall catch.

Even more convincing were the results of a similar analysis in which weight and hence the growth function's parameters were expressed in terms of value. For any level of natural mortality (observing the restriction imposed by the absolute commercial minimum presently in effect), maximum yield in value is attained when fishing commences at a shrimp size perceptibly below that at which maximum yield in weight would be expected.

The questions tentatively answered by this study have far greater implications from an economic than from a biological standpoint. Still of great concern is the problem of resource maintenance. We are unquestionably in a better position to judge when, in the development of any age group, the harvesting of shrimp should begin so as to obtain maximum production therefrom. But it remains for us to evaluate that level of fishing which, for a given set of environmental conditions and for the shrimp resource as a whole, is most conducive to our ultimate objective: maximum equilibrium yield.

ACKNOWLEDGMENTS

The successful outcome of the Tortugas experiment must in large part be attributed to the unstinting efforts of those responsible for its implementation and completion. Acknowledgment is especially due Thomas J. Costello who guided the experiment's marking and recovery phases; credit for assistance in all aspects of the field work is extended to Bureau and industry personnel alike. The author also appreciates the assistance rendered by Charles H. Lyles, Jr. and George W. Snow, Branch of Statistics, who expedited the availability of certain commercial fishery statistics employed in the analysis. Special thanks go to Kenneth N. Baxter for his painstaking computation of estimates of fishing effort.

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STUDY OF LOSS AND DELAY OF SALMON PASSING ROCK ISLAND DAM, COLUMBIA RIVER, 1954–56

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ABSTRACT

To determine loss or delay of salmonids in passing Rock Island Dam on the Columbia River, and whether such loss or delay was associated with the right bank ladder, salmon were tagged and released both above and below the dam in 1954–56. They were subsequently observed passing through the fishways and recovered at upstream points. Most tagged fish released below the left and right bank fishway returned over the left, corresponding closely with the choice of ladders made by the untagged populations. Point estimates of sockeye salmon losses ranged from 0 to 42 percent. Tagging results (one season only) on spring chinook salmon indicated a loss of fish released below the right bank ladder, but no loss when total tag returns from below and above dam releases were compared; data failed to show that the dam caused losses of summer chinook. Tagged salmon released below the dam were delayed 2 to 4 days. Altering the right bank fishway may cause more fish to use it, but there is no clear evidence that such alterations will reduce overall loss or delay.

Rock Island Dam, completed in 1934, was the first dam built on the Columbia River. It is about 450 miles above the river's mouth in central Washington (fig. 1). A fishway was built at each end of the dam to pass anadromous fish and in 1936 a third was added near the middle of the dam to pass salmon observed congregating there. These ladders were the pool type, 20 feet wide, with a gradient of 1 to 10.

The dam was modified during 1951–53 by installing regulating gates in the spillway channel increasing the forebay elevation approximately 12 feet (fig. 2). Six new generating units were added in the powerhouse (located on the left side of the dam). These modifications necessitated changing the fishways to meet the new forebay level, and fish attraction flow was increased at the lower end of the left (looking downstream) ladder to counteract the effect of increased flow from the turbine units. Although fishery agencies requested changes at the lower end of the right ladder to provide better entrance conditions and additional attraction flow, nothing was done at the time. The entrance of the right ladder at three different water levels is shown in figure 3.

The Federal Power Commission, in granting a license amendment for the modification of Rock Island Dam, reserved the right to require altering the lower end of the right ladder if substantial evidence were presented that such alterations or modifications were required for effective conservation of fish life resources of the Columbia River. Any such altering was to begin before Dec. 1, 1960.

The size of anadromous fish runs passing Rock Island is shown in table 1. Fewer of the fish have used the right ladder since the dam was modified. During the period 1936–52, for example, the counts of salmon and steelhead at the three ladders were distributed as follows: Left ladder, 47.8 percent; center ladder, 22.5 percent; right ladder, 29.7 percent. For the period 1953–56 (after modification of the dam), the counts were these: Left ladder, 73.7 percent;

Note.—Approved for publication May 26, 1964.

center ladder, 11.6 percent; and right ladder, 14.7 percent.

This report describes tagging details and the results of experiments at Rock Island Dam to determine whether the dam caused loss or delay to these runs, and whether loss or delay was associated with the failure of fish to find and use the dam's right bank fishway.

TABLE 1.—*Chinook and sockeye salmon and steelhead trout counted at Rock Island Dam, 1933–56* [1]

Year	Number of fish counted		
	Chinook	Sockeye	Steelhead trout
1933	5,668	40,737	1,055
1934	7,115	2,227	583
1935	16,305	14,013	5,418
1936	7,290	16,500	2,373
1937	5,133	15,089	2,214
1938	5,795	17,095	2,399
1939 [2]	11,206	19,591	5,425
1940	9,512	27,093	5,220
1941	2,507	963	3,513
1942	6,833	16,340	3,693
1943	11,129	17,522	2,315
1944	3,364	5,035	1,338
1945	5,699	7,148	1,118
1946	9,981	45,030	1,779
1947	11,717	79,831	1,971
1948	7,083	84,184	2,360
1949	12,353	18,600	2,470
1950	10,348	50,134	1,852
1951	18,752	101,826	3,121
1952	20,121	114,349	2,883
1953	31,080	151,747	4,001
1954	33,283	91,234	5,406
1955	25,658	155,055	3,141
1956	25,085	92,443	1,540

[1] Silver salmon (*O. kisutch*) averaged about 60 fish per year during this period.

[2] Grand Coulee Dam blocked upriver migration commencing this year.

METHOD OF TAGGING

Preliminary experiments on tagging and methods of catching salmon were performed in 1953 followed by full-scale experiments in 1954 through 1956 on chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*). We planned to tag steelhead trout (*Salmo gairdneri*) but too few (17 to 32 each year) were captured and tagged for subsequent analysis.

Salmon were trapped at the upstream edge of the counting boards within the left and right fishways and at the upstream outlet of the left ladder. (Earlier attempts to catch quantities of fish for tagging below the dam were unsuccessful.) The trapped fish were transferred to tank trucks and hauled to the tagging sites located approximately 1,000 feet below the dam on each side of the river in 1954 and 1955. In 1956, tagged salmon were released off the downstream face of the dam close to the left or right ladder. The fish were lowered to water level in canvas bags filled with water (fig. 4). Forebay tag releases were from a trap located at the left ladder exit, and at sites on both sides of the river about 1 mile above the dam.

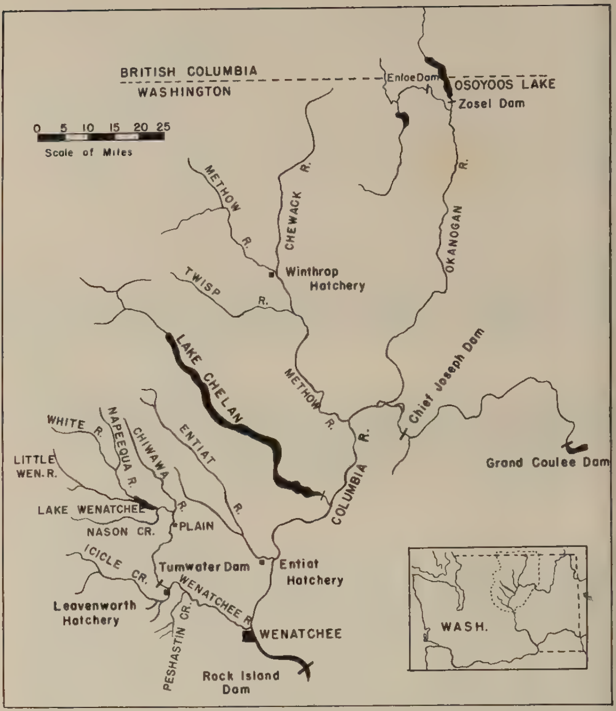

BRITISH COLUMBIA
WASHINGTON
EnloeDam
OSOYOOS LAKE
Zosel Dam
0 5 10 15 20 25
Scale of Miles
METHOW R.
CHEWACK R.
OKANOGAN R.
Winthrop Hatchery
TWISP R.
LAKE CHELAN
METHOW R.
Chief Joseph Dam
WHITE R.
NAPEEQUA R.
CHIWAWA R.
ENTIAT R.
COLUMBIA R.
LITTLE WEN. R.
Grand Coulee Dam
LAKE WENATCHEE
NASON CR.
PLAIN
ICICLE CR.
Tumwater Dam
Entiat Hatchery
WENATCHEE R.
Leavenworth Hatchery
PESHASTIN CR.
WENATCHEE
Rock Island Dam
WASH.

FIGURE 1.—Columbia River watershead between Rock Island and Grand Coulee Dams.

Various tag colors or shapes were used for the experiments at Rock Island Dam (fig. 5). Tags applied in the forebay differed from those used below the dam. Serially numbered plastic disks in combination with plastic bars formed one series of combinations, and serially numbered plastic disks with vinyl tubing and vinyl-coated nylon formed another series used below the dam. These were attached to each fish by nickel pins inserted through the body just below the dorsal fin. All tags were applied in pairs so that the same color or kind of tag showed on both sides of the fish. During 1954–55, the salmon were tagged while held in canvas-lined, cradle-type boxes. In 1956, the boxes were filled with water and the salmon were held under water during tagging.

Fish counters at the dam identified and recorded the tags as tagged fish crossed the counting boards. Display boards containing all tag samples were

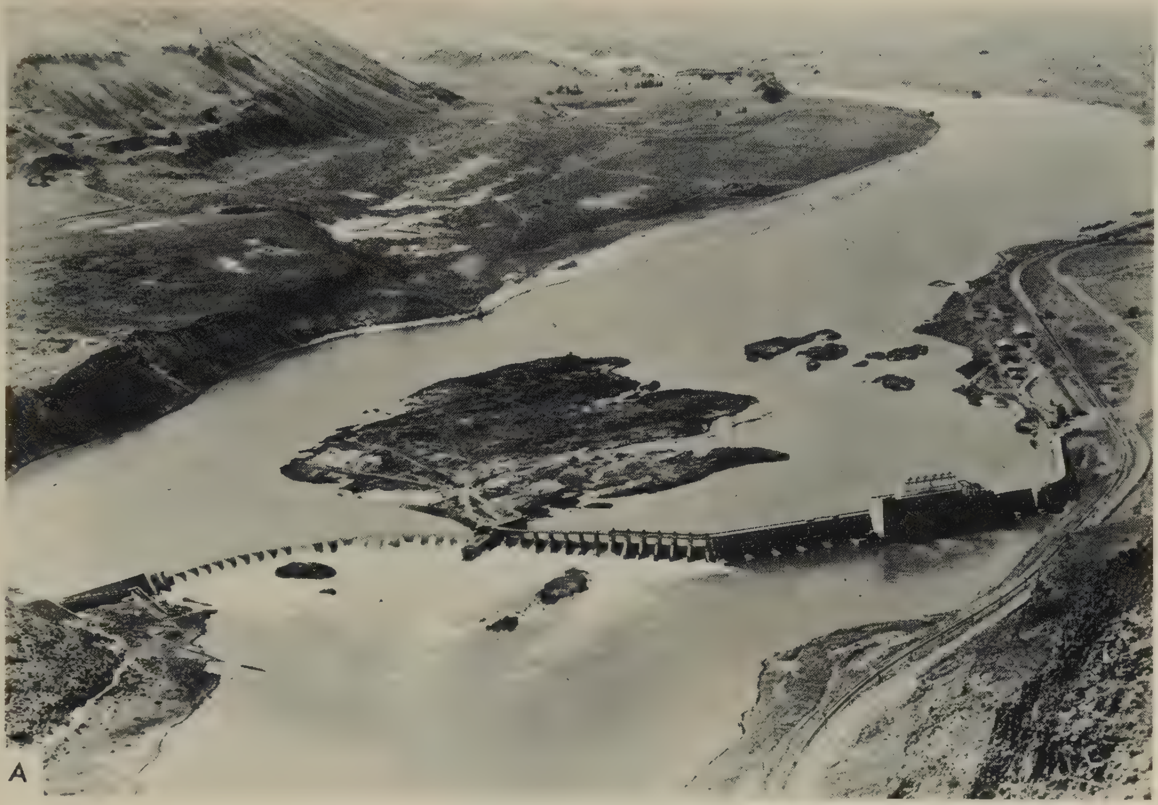


Figure 2a.—Rock Island Dam before modification.

placed in the counting rooms for reference but counters were not told of the tag applied each day.

Upstream tag recoveries were made from spawning ground surveys, at fish hatcheries, and from fish counters' observations at Tumwater and Zosel Dams (fig. 1). As different colors and combinations of tags were used for each experiment, a tag observed on a live fish provided the same information as an actual recovery, except for the identity of the particular fish. Therefore, upstream tag recoveries include both visual observations of tags and actual recoveries.

To determine mortalities at the dam, we analyzed and compared the percentage tag returns at Rock Island from releases below the left and right bank ladders; for upstream tag returns we compared recovery ratios from the different release areas above and below the dam. In addition, percentage tag returns from the two release areas below the dam were compared by date of tagging and by volume of water flow at Rock Island. To determine delay we computed the elapsed day-out (number of days between tagging and subsequent tag observations) periods of tag returns at Rock Island; for upstream returns we computed the difference in day-out periods for releases above and below the dam.

ESTIMATION OF TOTAL UPSTREAM RECOVERIES OF TAGGED SOCKEYE

Upstream tag recoveries and observations for the 1954–56 individual sockeye experiments at Rock Island are given in table 2. The numbers of tagged fish released are given by date, location, and age group. Releases at the four locations in the vicinity of the dam were designated as follows: below dam, left bank; below dam, right bank; above dam, left bank; above dam, right bank. The two age groups represented in the releases of tagged fish were 3-year-old sockeye, recognized by their small size, and sockeye over 3 years old. Most of the fish in the latter group were 4 years old; hence, this group is designated as 4-year-old sockeye.

The recoveries from each release lot are given by area of recovery above the dam: (1) Tumwater

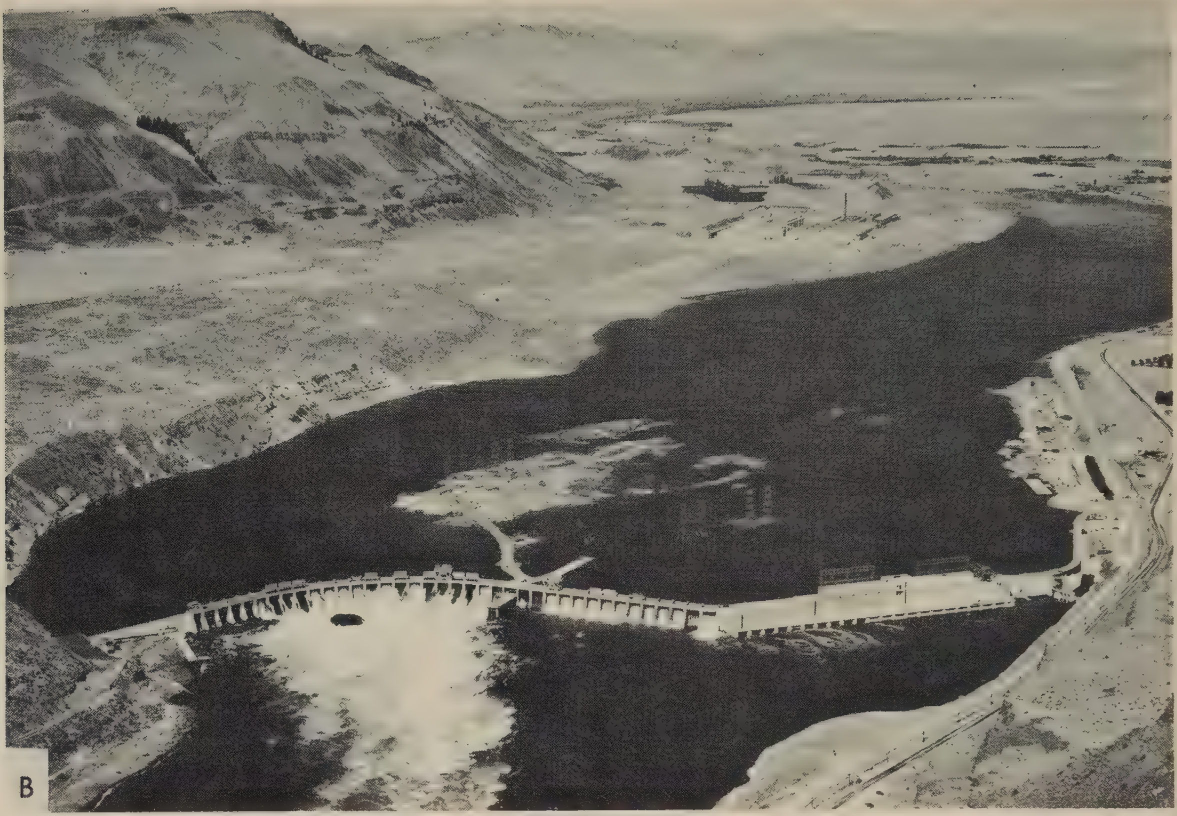


Figure 2b.—Rock Island Dam after modification.

Dam on the Wenatchee River; (2) Zosel Dam on the Okanogan River; (3) Okanogan River spawning grounds above Zosel Dam; and (4) all other areas combined.

In addition to the recovered tagged fish, numerous tagged sockeye were observed, but not recovered, in the recovery areas. These could be assigned to tagging date and release location, because different color combinations of tags were used for different release date-location combinations. They could not be individually assigned to age groups, however, hence, it is necessary to estimate the age composition of the tagged fish observed.

Spawning ground surveys of the Columbia River tributaries above Rock Island Dam indicated that 3-year-old sockeye migrate only to the Okanogan system, where they are found in varying numbers and proportions. On the basis of these surveys, together with the absence of recoveries of tagged 3-year-old sockeye in recovery areas 1 and 4, it is reasonable to assume that all the tagged fish observed in recovery areas 1 and 4 were 4-year-old sockeye.

The age composition of the tagged fish observed in recovery areas 2 and 3 can be estimated from proportions of 3-year-old sockeye in the recoveries from areas 2 and 3. Multiplying the proportions of 3-year-old sockeye in the recovery samples by the number of tagged fish observed provides estimates of the numbers of 3-year-old sockeye among the tagged fish observed. The numbers of 4-year-old sockeye among the tagged fish observed are obtained by subtraction. Table 3 shows the estimated numbers of 3- and 4-year-old sockeye observed in recovery areas 2 and 3.

In a number of instances, tagged sockeye recovered at Zosel Dam (recovery area 2) and released again after being checked for tag number and tag color were recovered a second time on the spawning grounds above Zosel Dam (recovery area 3). It is likely, therefore, that other tagged fish recovered or observed at Zosel Dam also were observed or recovered in recovery area 3. It is likely also that some tagged fish observed on the spawning grounds subsequently were recovered. Such double recoveries or observations result in a tagged fish being counted two or more times in recovery areas 2 and 3.

To estimate the number of tagged individuals in the recovery-observations totals, we use the following expression:

$$S=R_2+R_3+O_2+O_3-R_{23}-\frac{R_{23}}{R_2}(O_2)-\left(\frac{O_3}{R_3}\right)\left(\frac{R_{23}}{R_2}\right)(R_2+O_2)$$

Where, for each tag release group (age-release area-year combination),

R_2=number of tagged fish recovered at Zosel Dam
R_3=number of tagged fish recovered in area 3
O_2=number of tagged fish observed at Zosel Dam
O_3=number of tagged fish observed in area 3
R_{23}=number of tagged fish recovered at Zosel Dam and also in area 3

The first negative term corrects for double recoveries of tagged fish; the second negative term corrects for recoveries in area 3 of tagged fish observed at Zosel Dam; the last negative term corrects for observations in area 3 of tagged fish recovered or observed at Zosel Dam. The quantity, S, is referred to as the estimated total single recoveries.

Table 4 shows the recoveries, double recoveries, observations, estimated duplicate recovery-observations, and estimated total single recoveries for each release group.

Table 2.—*Sockeye salmon tagging data at Rock Island Dam*

[1954]

Area and date	Number released [1]	Number recovered								Number observed, age undetermined			
		3-year				4-year							
		Area of recovery				Area of recovery				Area where observed			
		1	2	3	4	1	2	3	4	1	2	3	4
Below dam, left bank:													
July 16	44 (2 42)	0	1	0	0	2	3	3	0	1	3	0	0
20	73 (7 66)	0	3	0	0	5	4	6	0	3	4	0	0
22	135 (27 108)	0	2	1	0	10	3	5	0	10	19	0	1
23	131 (21 110)	0	2	2	0	9	3	5	1	18	9	0	0
28	110 (20 90)	0	0	0	0	2	1	0	1	22	7	0	0
30	135 (62 73)	0	17	1	0	5	1	4	2	10	13	0	0
Aug. 6	125 (73 52)	0	6	2	0	3	0	0	1	6	16	1	0
11	31 (18 13)	0	0	0	0	2	0	0	0	1	0	2	0
13	18 (14 4)	0	1	0	0	0	0	0	1	0	2	0	0
Total	802 (244 558)	0	32	6	0	38	15	23	6	71	73	3	1
Below dam, right bank:													
July 1	1 (0 1)	0	0	0	0	0	0	0	0	0	0	0	0
7	7 (0 7)	0	0	0	0	1	0	0	0	0	0	0	1
8	14 (0 14)	0	0	0	0	0	0	0	0	1	0	1	0
21	126 (38 88)	0	2	0	0	2	3	2	1	7	23	1	0
22	25 (4 21)	0	0	0	0	1	0	0	1	2	2	1	0
27	83 (37 46)	0	2	1	0	0	0	1	1	10	18	0	0
29	63 (17 46)	9	4	1	0	3	1	0	1	6	9	0	0
Aug. 3	89 (43 46)	0	5	1	0	3	0	1	2	5	11	0	0
5	139 (82 57)	0	7	1	0	1	1	3	1	8	17	0	1
10	75 (43 32)	0	2	0	0	1	2	0	1	1	2	3	0
12	43 (25 18)	0	2	1	0	0	0	0	0	2	1	0	0
17	4 (1 3)	0	0	0	0	0	0	0	0	0	0	0	0
19	1 (0 1)	0	0	0	0	0	0	0	0	0	0	0	0
Total	670 (290 380)	0	24	5	0	12	7	7	8	42	83	6	2
Above dam, left bank:													
July 23	70 (14 56)	0	0	0	0	4	0	1	0	11	8	0	0
30	32 (8 24)	0	0	0	0	0	0	0	0	5	1	1	1
Aug. 4	30 (10 20)	0	0	1	0	1	0	0	0	7	4	0	0
6	13 (4 9)	0	0	0	0	0	0	0	0	1	0	0	0
13	8 (2 6)	0	0	0	0	0	0	0	1	0	0	2	0
20	2 (0 2)	0	0	0	0	0	0	0	0	0	0	0	0
27	2 (1 1)	0	0	0	0	0	0	0	0	0	0	0	0
Total	157 (39 118)	0	0	1	0	5	0	1	1	24	13	3	1
Summary:													
Below dam totals	1,472 (534 938)	0	56	11	0	50	22	30	14	113	156	9	3
Above dam totals [2]	157 (39 118)	0	0	1	0	5	0	1	1	24	13	3	1

See footnotes at end of table.

TABLE 2.—*Sockeye salmon tagging data at Rock Island Dam*—Continued

[1955]

Area and date	Number released [1]	Number recovered								Number observed, age undetermined			
		3-year				4-year				Area where observed			
		Area of recovery				Area of recovery							
		1	2	3	4	1	2	3	4	1	2	3	4
Below dam, left bank:													
July 21	59 (0 59)	0	0	0	0	9	2	8	0	1	0	2	0
26	111 (3 108)	0	0	1	0	14	2	9	1	3	0	1	1
28	95 (4 91)	0	0	0	0	24	1	5	0	2	0	1	1
29	92 (4 88)	0	0	0	0	20	3	4	1	1	0	1	0
Aug. 2	50 (3 47)	0	1	0	0	4	0	3	1	0	0	0	1
3	79 (3 76)	0	0	0	0	26	4	3	0	6	1	1	0
5	71 (11 60)	0	3	0	0	12	4	2	2	3	0	3	0
10	22 (4 18)	0	1	0	0	2	1	0	0	3	0	0	0
Total	579 (32 547)	0	5	1	0	111	17	34	5	19	1	9	3
Below dam, right bank:													
July 19	67 (1 66)	0	0	0	0	4	1	11	0	2	2	1	0
20	55 (2 53)	0	1	0	0	2	3	9	1	1	2	0	0
22	45 (4 41)	0	2	0	0	6	0	3	0	2	0	1	0
26	78 (5 73)	0	0	0	0	10	5	4	0	3	0	3	0
27	73 (3 70)	0	0	0	0	12	2	8	2	3	1	0	0
28	76 (5 71)	0	0	1	0	4	4	9	3	4	1	2	0
Aug. 2	24 (5 19)	0	0	0	0	4	1	1	0	1	0	1	0
4	101 (14 87)	0	1	0	0	16	5	1	1	1	0	2	0
9	41 (5 36)	0	0	0	0	6	1	2	0	2	0	0	1
11	37 (9 28)	0	1	0	0	5	0	0	0	3	0	0	0
Total	597 (53 544)	0	5	1	0	69	22	48	7	22	6	10	1
Above dam, left bank:													
July 21	61 (1 60)	0	0	0	0	8	4	8	1	7	0	0	0
29	60 (3 57)	0	0	0	0	5	2	5	0	2	0	2	0
Aug. 3	64 (1 63)	0	0	0	0	14	3	1	2	5	0	1	0
5	8 (1 7)	0	0	0	0	1	0	1	0	0	1	1	0
12	17 (5 12)	0	0	0	0	1	0	0	0	0	0	1	0
Total	210 (11 199)	0	0	0	0	29	9	15	3	14	1	5	0
Above dam, right bank:													
July 20	44 (1 43)	0	0	0	0	1	6	5	0	5	2	1	1
22	49 (2 47)	0	0	0	0	3	1	5	1	3	0	1	0
27	50 (3 47)	0	0	0	0	5	0	6	0	0	0	1	0
Total	143 (6 137)	0	0	0	0	9	7	16	1	8	2	3	1
Summary:													
Below dam total	1,176 (85 1,091)	0	10	2	0	180	39	82	12	41	7	19	4
Above dam total	353 (17 336)	0	0	0	0	38	16	31	4	22	3	8	1
[1956]													
Below dam, left bank:													
July 13	90 (1 89)	0	0	0	0	13	0	5	2	7	1	2	0
19	75 (15 60)	0	0	1	0	10	1	5	0	2	0	2	0
28	91 (38 53)	0	1	1	0	26	0	1	0	2	2	0	1
25	47 (9 38)	0	0	0	0	8	0	1	1	2	0	3	1
Aug. 1	41 (19 22)	0	0	1	0	4	1	1	0	0	2	0	0
3	49 (27 22)	0	2	0	0	2	0	0	1	3	2	4	0
Total	393 (109 284)	0	3	3	0	63	2	13	4	16	7	11	2
Below dam, right bank:													
July 10	24 (0 24)	0	0	0	0	2	0	0	1	1	0	3	0
12	20 (0 20)	0	0	0	0	0	0	0	0	0	0	5	0
17	80 (4 76)	0	0	0	0	10	0	5	0	2	1	9	0
24	75 (34 41)	0	2	2	0	15	0	2	0	1	0	1	0
26	96 (30 66)	0	0	0	0	27	0	2	0	2	0	1	0
31	33 (15 18)	0	0	1	0	4	0	0	0	1	1	2	0
Aug. 2	30 (24 6)	0	2	1	0	2	0	0	0	0	2	0	0
Total	358 (107 251)	0	4	4	0	60	0	9	1	7	4	21	0
Above dam, left bank:													
July 11	41 (0 41)	0	0	0	0	3	0	5	1	5	0	0	0
20	98 (21 77)	0	0	0	0	30	0	3	2	5	0	0	0
25	90 (36 54)	0	1	0	0	15	0	3	0	6	1	0	0
27	73 (26 47)	0	1	2	0	21	0	0	1	2	0	1	1
31	35 (19 16)	0	2	0	0	4	0	0	1	1	1	1	0
Aug. 1	19 (5 14)	0	0	1	0	5	0	0	0	0	0	0	0
2	46 (25 21)	0	1	1	0	4	0	0	0	0	1	1	1
Total	402 (132 270)	0	5	4	0	82	0	11	5	19	3	3	2
Above dam, right bank:													
July 18	19 (3 16)	0	0	0	0	3	0	1	0	0	0	0	0
Total	19 (3 16)	0	0	0	0	3	0	1	0	0	0	0	0
Summary:													
Below dam totals	751 (216 535)	0	7	7	0	123	2	22	5	23	11	32	2
Above dam totals	421 (135 286)	0	5	4	0	85	0	2	5	3	19	3	2

[1] Figures in parentheses represent the number of 3- and 4-year-old fish, respectively, making up the total.

[2] No tagged fish were released above dam, right bank, in 1954.

Table 5 contains a summary of releases of tagged sockeye by age group and release area and recoveries at Tumwater Dam, in the Okanogan River, and in other areas combined. The estimated total recoveries of 3- and 4-year-old tagged sockeye in the Okanogan system also are shown.

DETERMINATION OF MORTALITIES AT ROCK ISLAND

If there were a substantial loss of fish below Rock Island Dam, whether caused by a failure of fish to find a fish ladder or for other reasons, there should be a greater upstream recovery of fish tagged and released above the dam than of fish similarly tagged and released below the dam. Mortalities also should be reflected by the number of tagged fish passing the dam compared to the number released. We found, as shown later, that the fish counters' records of tagged fish passing Rock Island Dam from releases below the dam did not give completely reliable data on fish mortalities (assuming unaccounted-for tags as mortalities caused by the dam). Results of the upstream tag recovery comparisons are presented first, followed by the results obtained at Rock Island Dam.

RETURNS FROM UPSTREAM

Sockeye

Analysis of the tagging data to estimate mortalities is complicated by the presence of different races of sockeye in the tagging groups, by different age groups, and by the unequal effort expended recovering tags from different races and age groups. The sockeye run separates a short distance above Rock Island Dam, with some fish going into the Wenatchee River system and some fish up the Columbia River to the Okanogan River system. A few sockeye show up at the Entiat and Winthrop fish hatcheries and in Icicle Creek below the Leavenworth fish hatchery. As stated previously, 3-year-old sockeye are restricted to the Okanogan system and 4-year-old fish are found in all areas. We could effectively observe or recover all tagged fish passing Tumwater Dam on the Wenatchee River while on the way to spawning areas. In the Okanogan system, however, tag recoveries were made during stream surveys of the spawning areas and sampling at Zosel Dam on the Okanogan River. Thus, the recovery effort for tags on fish in the Wenatchee and Okanogan systems was not equal. Adding to these complications is the very probable loss of some tagged fish due to a tagging mortality or to straying.

Taking a simple approach, we have estimated the mortality rates from the ratios of the recovery proportions of tagged fish recovered from above- and below-dam releases. We made the following general assumptions: (1) The chance of recovering tagged fish is the same regardless of tagging date and tagging site, (2) racial proportions in the tagging lots are the same for the different areas of release, and (3) the chance of a tag recovery or observation is independent of tag type or color.

TABLE 3.—*Estimated numbers of 3- and 4-year-old tagged sockeye salmon in recovery areas 2 and 3, by year and release area*

Year and release area	Recovery Area 2										Recovery Area 3									
	Number recovered			Per-cent 3's	Number observed	Estimated numbers observed		Estimated totals			Number recovered			Per-cent 3's	Number observed	Estimated numbers observed		Estimated totals		
	3's	4's	Total			3's	4's	3's	4's	Totals	3's	4's	Total			3's	4's	3's	4's	Total
1954																				
Below dam, left bank	32	15	47	68	73	50	23	82	38	120	6	23	29	21	3	1	2	7	25	32
Below dam, right bank	24	7	31	77	83	64	19	88	26	114	5	7	12	42	6	2	4	7	11	18
Above dam, left bank	0	0	0	--------	13	~7	~6	7	6	13	1	1	2	50	3	1	2	2	3	5
1955																				
Below dam, left bank	5	17	22	23	1	0	1	5	18	23	1	34	35	3	9	0	9	1	43	44
Below dam, right bank	5	22	27	18	6	1	5	6	27	33	1	48	49	2	10	0	10	1	58	59
Above dam, left bank	0	9	9	0	1	0	1	0	10	10	0	15	15	0	5	0	5	0	20	20
Above dam, right bank	0	7	7	0	2	0	2	0	9	9	0	16	16	0	3	0	3	0	19	19
1956																				
Below dam, left bank	3	2	5	60	7	4	3	7	5	12	3	13	16	19	11	2	9	5	22	27
Below dam, right bank	4	0	4	100	4	4	0	8	0	8	4	9	13	31	21	6	15	10	24	34
Above dam, left bank	5	0	5	100	3	3	0	8	0	8	4	11	15	27	3	1	2	5	13	18
Above dam, right bank	0	0	0	--------	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1

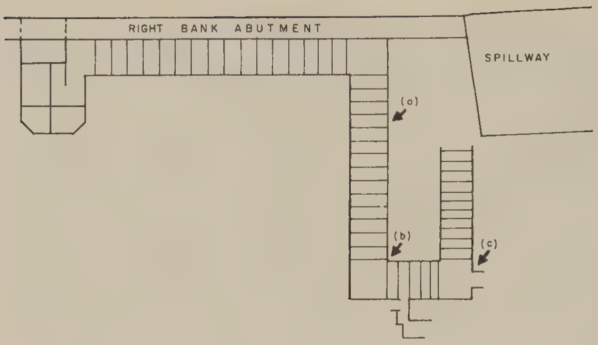


FIGURE 3.—Lower end of right ladder at different water levels. Diagrammatic sketch shows photo areas: (a) high flows; (b) intermediate flows; and (c) low flows.

The estimating equation for survival rate (k) is given by

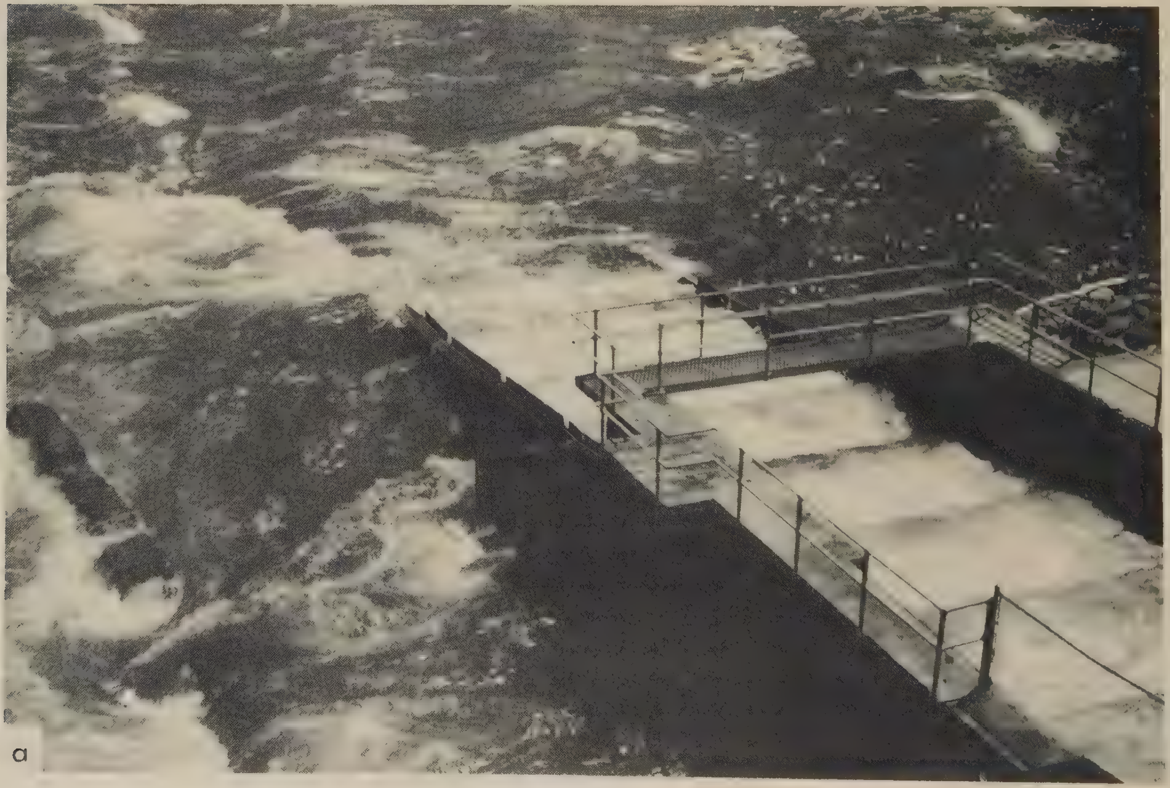
$$\frac{R_b/T_b}{R_a/T_a}$$

where

T_b = Number of tagged fish released below dam
R_b = Number of tagged fish recovered from T_b
T_a = Number of tagged fish released above the dam
R_a = Number of tagged fish recovered from T_a

If the value of the ratio is one then mortality is zero. Where the value of this ratio is less than one, then the corresponding mortality rate is given by $1-k$.

The results of tagging experiments on the 3-year-old sockeye are shown in table 6. It is apparent that too few 3-year-old sockeye were tagged above the dam to afford meaningful comparisons between above and below dam experiments and to give estimates of mortality rates. No mortalities were evident from the limited data available. A comparison of the recovery proportions of tagged fish released below the left and right fishways shows right bank releases having a higher recovery rate in 2 of the 3 years. For all years combined the two recovery rates were nearly identical.



b

c

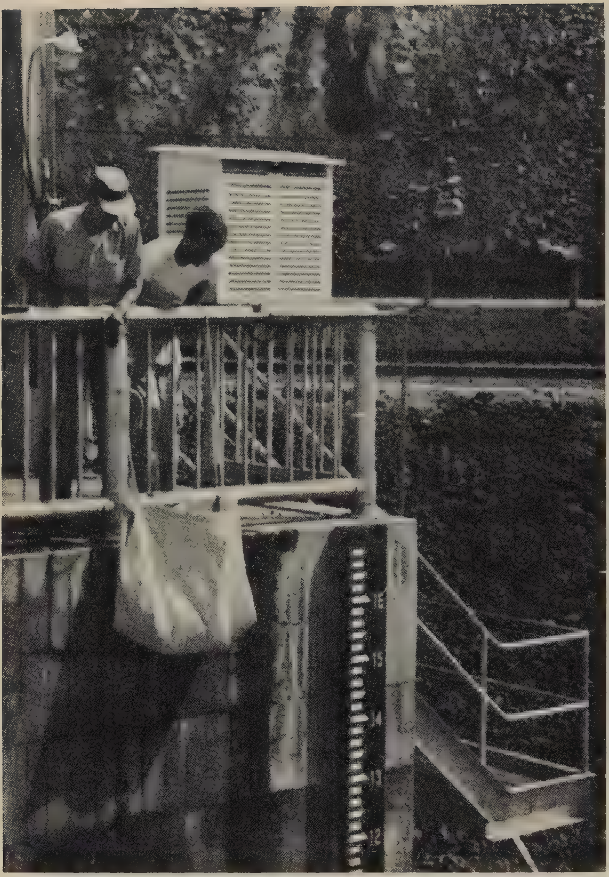


FIGURE 4.—Lowering tagged fish off the deck of the dam.

In table 7 are listed the estimates of mortalities based on all 4-year-old sockeye recoveries.

Compared with the proportions of tagged fish recovered from the area AL (left bank above the dam) releases, tagged fish released on the left bank below the dam suffered mortalities of about 10, 6, and 16 percent in 1954, 1955, and 1956, respectively. Tagged fish released on the right bank below the dam suffered mortalities of about 22, 12, and 18 percent in the corresponding years. We would conclude from these point estimates that tagged fish released below the dam suffered a mortality due to the dam, and that the mortality rate was greater for fish released on the right bank below the dam than for fish released on the left bank below the dam.

Compared with the proportions of tagged fish recovered from the AR (right bank above the dam) releases, tagged fish released on the left bank below the dam suffered no mortality due to the dam in either 1955 or 1956. Neither did tagged fish released on the right bank below the dam. The point estimates for 1956, it should be recognized, are based on a release of only 16 fish in area AR.

In combining the data for the 3 years, we could conclude, on the basis of recoveries from area AL releases, that tagged fish released on the left bank below the dam suffered a mortality of about 16 percent because of the dam, and that tagged fish released on the right bank below the dam suffered a mortality of about 21 percent because of the dam. Little or no mortality was indicated on the basis of releases in area AR (0 and 2 percent).

When comparing proportions of tagged fish recovered from total releases below the dam with all releases above the dam, we obtained point estimates of mortalities due to the dam of about 15 percent in 1954, 4 percent in 1955, 15 percent in 1956, and 15 percent for all years.

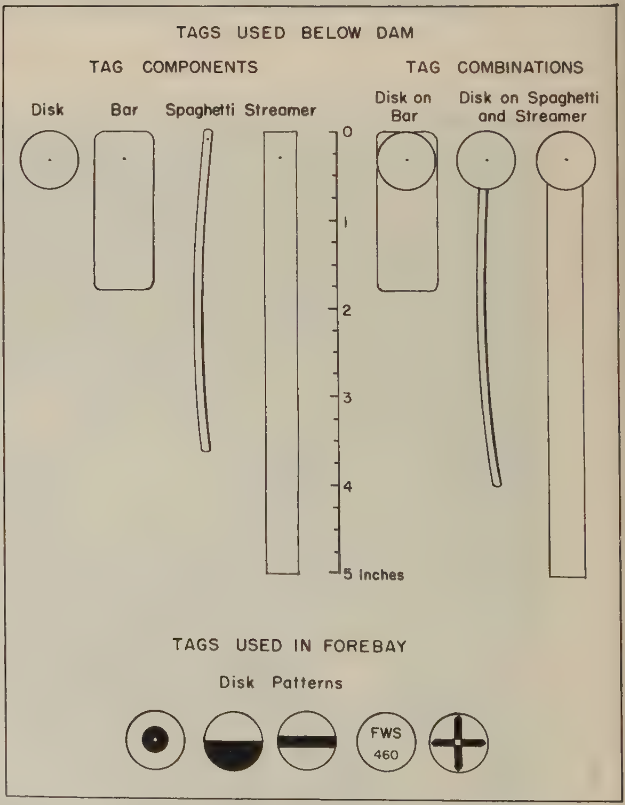


FIGURE 5.—Kinds of tags used during the Rock Island tagging experiments.

TABLE 4.—*Estimates of total single recoveries in the Okanogan system by age group and release area, Rock Island Dam sockeye tagging, 1954–56*

Year and release area	Number recovered area 2 (R_2)	Number recovered area 3 (R_3)	Number observed area 2 (O_2)	Number observed area 3 (O_3)	$R_2+R_3+O_2+O_3$	Number recovered second time in area 3 (R_{23})	$\frac{R_{23}}{R_2}(O_2)$	$\frac{O_3}{R_3}\left(\frac{R_{23}}{R_2}\right)(R_2+O_2)$	Total correction	Estimated total single recoveries (S)
	3-year-old sockeye									
1954										
Below dam, left bank	32	6	50	1	89	1	2	0	3	86
Below dam, right bank	24	5	64	2	95	0	0	0	0	95
Above dam, left bank	0	1	7	1	9	0	0	0	0	9
1955										
Below dam, left bank	5	1	0	0	6	0	0	0	0	6
Below dam, right bank	5	1	1	0	7	0	0	0	0	7
Above dam, left bank	0	0	0	0	0	0	0	0	0	0
Above dam, right bank	0	0	0	0	0	0	0	0	0	0
1956										
Below dam, left bank	3	3	4	2	12	0	0	0	0	12
Below dam, right bank	4	4	4	6	18	0	0	0	0	18
Above dam, left bank	5	4	3	1	13	0	0	0	0	13
Above dam, right bank	0	0	0	0	0	0	0	0	0	0
	4-year-old sockeye									
1954										
Below dam, left bank	15	23	23	2	63	3	5	1	9	54
Below dam, right bank	7	7	19	4	37	0	0	0	0	37
Above dam, left bank	0	1	6	2	9	0	0	0	0	9
1955										
Below dam, left bank	17	34	1	9	61	2	0	1	3	58
Below dam, right bank	22	48	5	10	85	1	0	0	1	84
Above dam, left bank	9	15	1	5	30	0	0	0	0	30
Above dam, right bank	7	16	2	3	28	1	0	0	1	27
1956										
Below dam, left bank	2	13	3	9	27	1	2	2	5	22
Below dam, right bank	0	9	0	15	24	0	0	0	0	24
Above dam, left bank	0	11	0	2	13	0	0	0	0	13
Above dam, right bank	0	1	0	0	1	0	0	0	0	1

We observe from the estimated confidence limits that the lower limits bracket zero in most instances and range to about 5 percent. The upper limits range from 20 to about 46 percent.

Another procedure was to estimate mortality rates based on recoveries of 4-year-old sockeye at Tumwater Dam (table 8). Compared with the proportions of tagged fish recovered from area AL (left bank above the dam) releases, tagged fish from left bank-below releases suffered mortalities of about 21, 0, and 26 percent, respectively, for 1954, 1955, and 1956. Tagged fish released on the right bank below the dam suffered mortalities of about 42, 23, and 29 percent, respectively, for the same 3 years.

Compared with the proportions of tagged fish recovered from the area AR releases (right bank above the dam), the tagged fish released at the right and left banks below the dam suffered no mortalities.

Combining the data for the 3 years, we observe on the basis of area AL releases that tagged fish released below the left fishway suffered a mortality of about 22 percent and that tagged fish released below the right bank fishway suffered a mortality of about 39 percent. No mortality was indicated on the basis of releases in area AR; however, comparatively few fish were released there.

Point estimates of mortality rates, obtained from comparisons of proportions of tagged fish recovered from total releases below the dam with all releases above the dam are about 29 percent in 1954, 0 percent in 1955, 25 percent in 1956, and 21 percent for all years.

Considering the confidence limits of these mortality rates based on Tumwater Dam recoveries, we observe the lower limits to bracket zero in two instances and range to 28 percent. The upper limits range from about 32 to 66 percent.

It is readily apparent that the analyses of the sockeye tagging data gave conflicting results of mortalities caused by the dam. On the one hand, many experiments indicated substantial mortalities, and mortalities apparently were greater for fish released below the right bank fishway. On

Table 5.—*Summary of Rock Island Dam sockeye tagging data by age group, 1954–56*

Year and release area	Total number released	3-year-old sockeye		4-year-old sockeye				Estimated total Okanogan recoveries
		Number released	Estimated number recovered in Okanogan	Number released	Number recovered			
					Tumwater	Estimated in Okanogan	Other areas	
1954								
Below dam, left bank	802	244	86	558	109	54	7	140
Below dam, right bank	670	290	95	380	54	37	10	132
Total	1,472	534	181	938	163	91	17	272
Above dam, left bank	157	39	9	118	29	9	2	18
Total	157	39	9	118	29	9	2	18
1955								
Below dam, left bank	579	32	6	547	130	58	8	64
Below dam, right bank	597	53	7	544	91	84	8	91
Total	1,176	85	13	1,091	221	142	16	155
Above dam, left bank	210	11	0	199	43	30	3	30
Above dam, right bank	143	6	0	137	17	27	2	27
Total	353	17	0	336	60	57	5	57
1956								
Below dam, left bank	393	109	12	284	79	22	6	34
Below dam, right bank	358	107	18	251	67	24	1	42
Total	751	216	30	535	146	46	7	76
Above dam, left bank	402	132	13	270	101	13	7	26
Above dam, right bank	19	3	0	16	3	1	0	1
Total	421	135	13	286	104	14	7	27
Totals 1954–55–56								
Below dam, left bank	1,774	385	104	1,389	318	134	21	238
Below dam, right bank	1,625	450	120	1,175	212	145	19	265
Total	3,399	835	224	2,564	530	279	40	503
Above dam, left bank	769	182	22	587	173	52	12	74
Above dam, right bank	162	9	0	153	20	28	2	28
Total	931	191	22	740	193	80	14	102

the other hand, many of the experiments indicated no mortalities caused by the dam.

Returns from below the dam by date of tagging.—The upstream recoveries of tagged sockeye, released below the dam, indicated a fairly uniform pattern of returns for all experiments (figs. 6,7, and 8). As tagging experiments were alternated between left and right banks on alternate days, these graphs show a fairly consistent pattern of returns for both release areas and for the duration of the tagging season. The percent-recovered curve in 1954 assumed the shape of the numbers-tagged curve, with fewer returns from the tails of the experiments. Percentage returns for 1955 and 1956 show a remarkably uniform pattern. The large numbers tagged, shown for July 26 and 28 in 1955 and for July 24 in 1956, are the result of combining left and right bank experiments, as experiments were conducted on both banks on those dates. Returns of nearly 50 percent from the August 3, 1955, experiment (fig. 7) are a result of observing a large number of that day's tagged fish passing Tumwater Dam, more fish observed than for any other single experiment. It might be that this particular sample contained relatively more Wenatchee fish than the other samples.

Returns from below dam compared with water flow.—In order to determine the influence of different water levels on fish passage at Rock Island Dam, tag recoveries from releases at each bank below the dam were compared with water flow (figs. 9, 10, and 11). In general, the tag returns from both banks showed a fairly consistent pattern despite large changes in flow during the experiments.

The returns for 1954 merit attention, since fewer returns are indicated for experiments on August 10–13 during the low river flows (fig. 9). These

TABLE 6.—*Estimated mortality rates due to Rock Island Dam based on 3-year-old sockeye tag recoveries*

Year and release area	Number released	Estimate number recovered	Proportion recovered r_i	Estimate of mortality rates				
				$1-\frac{r_{BL}}{r_{AL}}$	$1-\frac{r_{BL}}{r_{AR}}$	$1-\frac{r_{BR}}{r_{AL}}$	$1-\frac{r_{BR}}{r_{AR}}$	$1-\frac{r_{BL}+r_{BR}}{r_{AL}+r_{AR}}$
1954								
Below dam, left bank	244	86	0.352	−0.524				
Below dam, right bank	290	95	.328			−0.420		
Total	534	181	.339					−0.468
Above dam, left bank	39	9	.231					
Total	39	9	.231					
1955								
Below dam, left bank	32	6	.188					
Below dam, right bank	53	7	.132					
Total	85	13	.153					
Above dam, left bank	11	0	0					
Above dam, right bank	6	0	0					
Total	17	0	0					
1956								
Below dam, left bank	109	12	.110	−.122				
Below dam, right bank	107	18	.168			−.714		
Total	216	30	.139					−.448
Above dam, left bank	132	13	.098					
Above dam, right bank	3	0	0					
Total	135	13	.096					
Totals *1954–55–56*								
Below dam, left bank	385	104	.270	−1.231				
Below dam, right bank	450	120	.267			−1.207		
Total	835	224	.268					−1.330
Above dam, left bank	182	22	.121					
Above dam, right bank	9	0	0					
Total	191	22	.115					

fewer returns undoubtedly are related to a diminished effort to recover tags from these experiments. Fish counting and tag observing were discontinued at Zosel Dam from August 20 to August 26, at a time when tagged fish were still passing and when the number of tags from the August 10–13 experiments should have peaked there. Therefore, with comparable recovery effort, tag returns from these experiments probably would have been greater than indicated. It is noted that the 1955 returns from this same time period, August 9–11, and for comparable water flows (fig. 10), were consistent with returns from earlier experiments occurring at high flows. It is evident, as shown by upstream tag returns, that changes in flows at Rock Island Dam had little effect on the ability of sockeye to pass the dam.

Chinook

In order to compare recovery ratios of chinook salmon tagged above and below the dam, it was necessary to separate the chinooks by race. Races at Rock Island Dam were reported by Fish and Hanavan (1948) as spring and summer chinook. Spring chinook, passing Rock Island Dam earlier in the season than summer chinook, migrated to smaller, more remote spawning streams. In these streams, tagged fish were much easier to observe and recover than in larger streams, such as the Wenatchee and lower Methow Rivers (the summer chinook spawning areas). Thus, recoveries from spring chinook tagging experiments were much greater than from experiments on summer chinook.

Upstream tag recoveries for all chinook experiments are given in table 9. Many samples were too small to compare returns statistically. Only in 1956 were sufficient fish obtained to release at the two banks below the dam and above the dam. Returns of spring chinooks tagged below the dam were virtually the same (27 percent) for the 3

TABLE 7.—*Estimated mortality rates due to Rock Island Dam based on total 4-year-old sockeye recoveries*

[95 percent confidence limits]

Year and release area	Number released	Estimate number recovered	Proportion recovered r_i	Estimates of mortality rates				
				$1-\frac{r_{BL}}{r_{AL}}$	$1-\frac{r_{BL}}{r_{AR}}$	$1-\frac{r_{BR}}{r_{AL}}$	$1-\frac{r_{BR}}{r_{AR}}$	$1-\frac{r_{BL}+r_{BR}}{r_{AL}+r_{AR}}$
1954								
Below dam, left bank	558	170	0.305	0.100 (−0.159 to 0.359).				
Below dam, right bank	380	101	.266			0.215 (−0.028 to 0.458).		
Total	938	271	.289					0.147 (−0.089 to 0.383).
Above dam, left bank	118	40	.339					
Total	118	40	.339					
1955								
Below dam, left bank	547	196	.358	0.064 (−0.136 to 0.264).	−0.065			
Below dam, right bank	544	183	.336			0.120 (−0.071 to 0.311).		
Total	1,091	379	.347					0.044 (−0.116 to 0.204).
Above dam, left bank	199	76	.382					
Above dam, right bank	137	46	.336					
Total	336	122	.363					
1956								
Below dam, left bank	284	107	.377	0.158 (−0.014 to 0.330).	−.508			
Below dam, right bank	251	92	.366			0.183 (0.008 to 0.358).	−0.464	
Total	535	199	.372					0.149 (0 to 0.298).
Above dam, left bank	270	121	.448					
Above dam, right bank	16	4	.250					
Total	286	125	.437					
Totals *1954–55–56*								
Below dam, left bank	1,389	473	.340	0.158 (0.053 to 0.263).	−.040			
Below dam, right bank	1,175	376	.320			0.208 (0.103 to 0.313).	0.022 (−0.221 to 0.265).	
Total	2,564	849	.331					0.147 (0.054 to 0.240).
Above dam, left bank	587	237	.404					
Above dam, right bank	153	50	.327					
Total	740	287	.388					

years. In 1956, returns from tagging at the right bank were considerably lower than those from the left bank; however, the reverse was true for 1955. No reasonable explanation can be offered for these differences. Perhaps conditions which may have caused low recoveries from the right bank one season were not present the other season, or it may have been chance that upstream recoveries varied as they did in the 2 years.

The data for 1956 indicated a loss of fish released below the right bank fishway when recovery proportions were compared to recovery proportions of fish released above the dam (19.5 percent compared to 24.4 percent). In terms of mortality rates, in the same manner as was done for the sockeye, this would indicate a 20 percent mortality for fish tagged below the right bank. No mortalities were indicated when comparing total returns from below the dam with returns from above the dam.

While summer chinook tag returns are comparatively few, the recovery ratios are consistent over the years and for the different areas of release. Only in 1954 was there an indication of mortalities for right bank tag releases (7.1 percent recovered compared with 7.8 percent recovered from above the dam). In the other 2 years there was no indication of mortalities. There was no indication

TABLE 8.—*Estimated mortality rates due to Rock Island Dam based on Wenatchee sockeye recoveries*

[95 Percent confidence limits]

Year and release area	Number released	Estimate number recovered	Proportion recovered r_i	Estimates of mortality rates and confidence limits				
				$1-\frac{r_{BL}}{r_{AL}}$	$1-\frac{r_{BL}}{r_{AR}}$	$1-\frac{r_{BR}}{r_{AL}}$	$1-\frac{r_{BR}}{r_{AR}}$	$1-\frac{r_{BL}+r_{BR}}{r_{AL}+r_{AR}}$
1954								
Below dam, left bank	558	109	0.195	0.207 (0.08 to 0.497).				
Below dam, right bank	380	54	.142			0.423 (0.186 to 0.660).		
Total	938	163	.174					0.293 (0.044 to 0.542).
Above dam, left bank	118	29	.246					
Total	118	29	.246					
1955								
Below dam, left bank	547	130	.238	−0.102	−0.919			
Below dam, right bank	544	91	.167			0.227 (−0.030 to 0.484).	−0.347	
Total	1,091	221	.203					−0.134.
Above dam, left bank	199	43	.216,					
Above dam, right bank	137	17	.124,					
Total	336	60	.179					
1956								
Below dam, left bank	284	79	.278	0.257 (0.072 to 0.442).	−.479			
Below dam, right bank	251	67	.267			0.286 (0.099 to 0.473).	−.420	
Total	535	146	.273					0.250 (0.089 to 0.411).
Above dam, left bank	270	101	.374					
Above dam, right bank	16	3	.188					
Total	286	104	.364					
Total, *1954–55–56*								
Below dam, left bank	1,389	318	.229	0.224 (0.099 to 0.349).	−.748			
Below dam, right bank	1,175	212	.180			0.390 (0.280 to 0.500).	−.374	
Total	2,564	530	.207					0.207 (0.092 to 0.322).
Above dam, left bank	587	173	.295					
Above dam, right bank	153	20	.131					
Total	740	193	.261					

TABLE 9.—*Upstream returns of tagged spring and summer chinook by area of released at Rock Island Dam, 1954–56*

Year and release area	Spring chinook			Summer chinook		
	Tagged	Recovered		Tagged	Recovered	
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*
1954						
Below dam, right bank	150	40	26.7	113	8	7.1
Below dam, left bank				80	7	8.8
Total below dam	150	40	26.7	193	15	7.8
Above dam				217	17	7.8
1955						
Below dam, right bank	122	38	31.1	66	10	15.2
Below dam, left bank	70	13	18.6	34	2	5.9
Total below dam	192	51	26.6	100	12	12.0
Above dam	3	1	33.3	99	9	9.1
1956						
Off dam, right side	159	31	19.5	92	11	12.0
Off dam, left side	154	53	34.4	113	11	9.7
Total off dam	313	84	26.8	205	22	10.7
Above dam	168	41	24.4	199	21	10.6

of mortalities when comparing total returns from above and below the dam.

In view of these similar recoveries of tagged chinook salmon released above and below Rock Island Dam, we cannot conclude that there is a substantial mortality caused by the dam. For spring chinooks, there are indications of a loss of fish released below the right bank ladder in 1956. Data are not available for determining if this loss exists for the other 2 years.

RETURNS AT ROCK ISLAND

Identity of Tags and Species

The correct identity of tag returns at Rock Island Dam depended upon the fish counters'

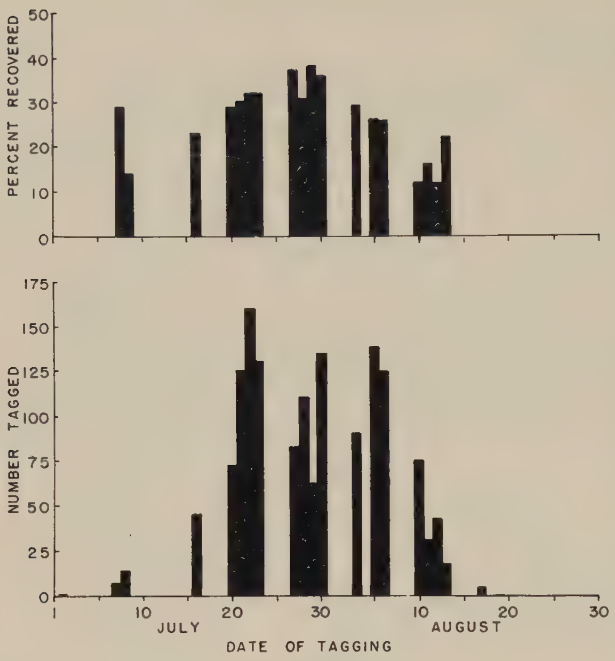


FIGURE 6.—Numbers of sockeye tagged below Rock Island Dam, and recoveries of tagged fish upstream, expressed as percentages of the number tagged each day, 1954.

identifying accurately the various tags and species of fish as the fish crossed counting boards. The tags were more difficult to identify at Rock Island than at upstream points because of the need for counting large numbers of fish while simultaneously identifying tags, and because of the speed the fish moved across the counting boards. The misidentification of both tags and species was a source of error in the Rock Island tag return data as exemplified in the following illustrations:

1. In some of the 1954 experiments, fish counters recorded as tagged species which had not been tagged. In other experiments, they recorded greater numbers of tag observations of species than fish tagged, and on several occasions they counted fewer jack chinook in the traps than were tallied during subsequent tagging. We revised our tagging procedure for some experiments in 1954 to determine the magnitude of error in species identification. Instead of tagging all species with one color combination as was usually done, we tagged the various species with different color combinations and noted the returns as identified by the counters (table 10). Many chinooks (obviously jacks) were called sockeye. Jacks are precocious male chinooks, and are similar in size to sockeye. The error in mistaking sockeye for chinooks was relatively small. No tagged steelhead were reported by the counters at Rock Island Dam; one tagged steelhead, however, was observed upstream at Tumwater Dam. Similar errors were made in 1955 and 1956, although the fish counters were asked to keep the counting boards at the minimum depth consistent with efficient fish passage. The magnitude of error was not determined for these years.

2. The disproportionate returns of the different types of tags used gave evidence of errors in tag identity at Rock Island Dam. A far greater percentage of bar tags was observed at Rock Island in 1954 and 1955 than of spaghetti tags (table 11). Upstream, however, the percentage returns of the two tags were approximately the same for both years. The streamer tag was substituted

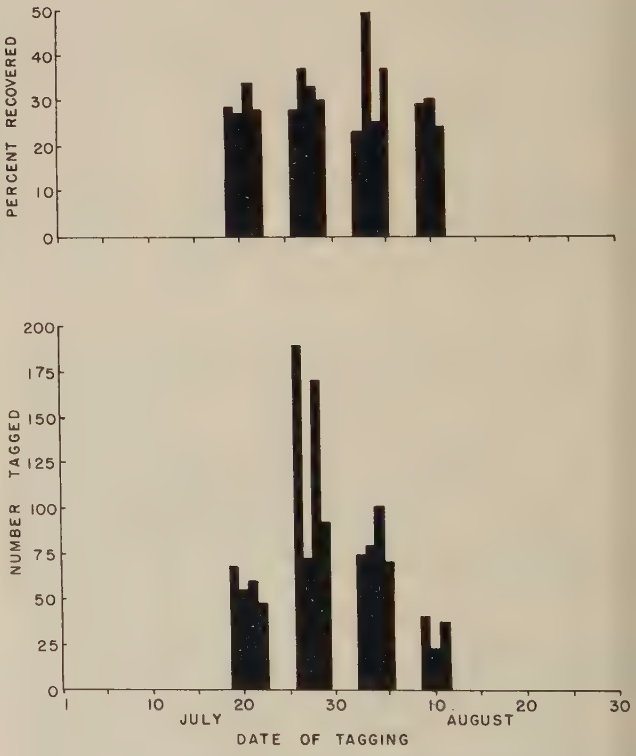


FIGURE 7.—Numbers of sockeye tagged below Rock Island Dam, and recoveries of tagged fish upstream, expressed as percentages of the number tagged each day, 1955.

for the spaghetti tag in 1956, and, as observed, returns were similar at Rock Island Dam and upstream for the two tags. It is evident, therefore, that the counters at Rock Island Dam did not discriminate between the tags in 1954 and 1955.

TABLE 10.—*Errors in species identification at Rock Island Dam in 1954*

Species and date tagged	Tagged	Species reported by counters	Error
	Number	*Number*	*Percent*
Chinook:			
Aug. 5[1]	6	0	
6	11	2 chinook 4 sockeye	66.7
10	20 chinook 2 steelhead	4 chinook 9 sockeye	69.2
11	13 chinook 2 steelhead	2 chinook 10 sockeye	83.4
Total	50 chinook 4 steelhead	10 chinook 24 sockeye	70.5
Sockeye:			
Aug. 5	139	136 sockeye 1 chinook	0.7
6	125	90 sockeye	0
10	75	71 sockeye[2] 8 chinook	10.1
11	31	22 sockeye 2 chinook	8.3
Total	370	319 sockeye 11 chinook	3.3

[1] The color and tag combination used here was also used 15 days previous. Some returns may have been attributed to the previous experiment.

[2] The total of 79 fish observed is an obvious error in tag identity.

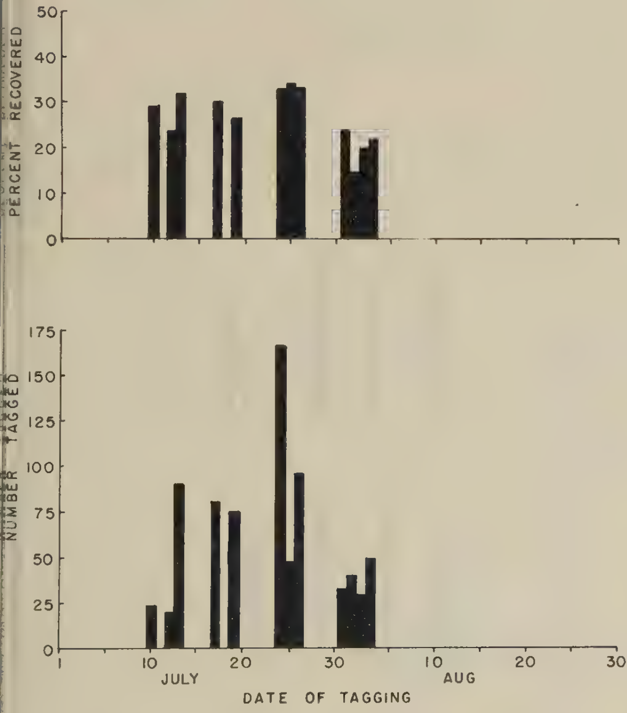


FIGURE 8.—Numbers of sockeye tagged below Rock Island Dam, and recoveries of tagged fish upstream, expressed as percentages of the number tagged each day, 1956.

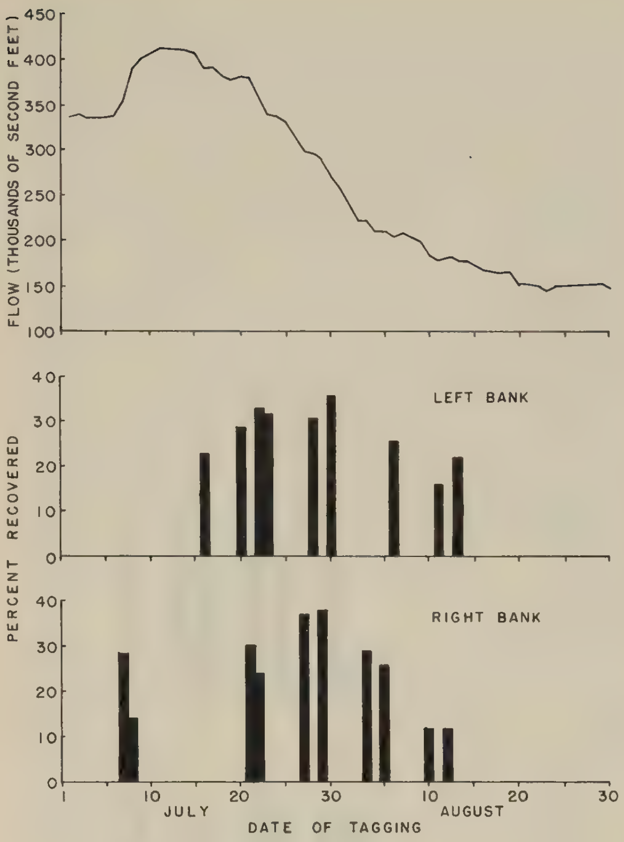


FIGURE 9.—Recoveries of tagged sockeye upstream expressed as percentages of the number tagged at each bank below, compared with water flow, 1954.

These errors in species and tag identification thus affected the reliability of the tag return data at Rock Island Dam, and the data must be used with caution.

Sockeye and Chinook

The results of the fish counters' observations of tagged fish (including the few steelhead tagged) crossing the counting boards for the four seasons of tagging are shown in table 12. Although the salmon were released below the dam at various places on both sides of the river, most of the tags were observed at the left ladder. Comparatively few were recorded at the right ladder, even though roughly half of the salmon were released a short distance away. The counters observed 85 percent of the tags at the left and center ladders for the 4 years. While only 64 to 86 percent of the fish released below the dam were observed at the counting boards, we cannot say with certainty that these missing tags indicated mortalities caused by the dam.

These are some possible reasons for the apparent tag losses:

1. Counters did not identify tagged fish crossing the counting boards.
2. Tagging harmed the fish.
3. Fish lost the tags.
4. Tagged fish refused to re-pass the dam.
5. The dam itself caused mortalities.

The counters did overlook tagged salmon. On a few occasions when the forebay trap was fished, we captured tagged fish the counters had not reported. In some experiments, we recovered more tags upstream than the counters reported at

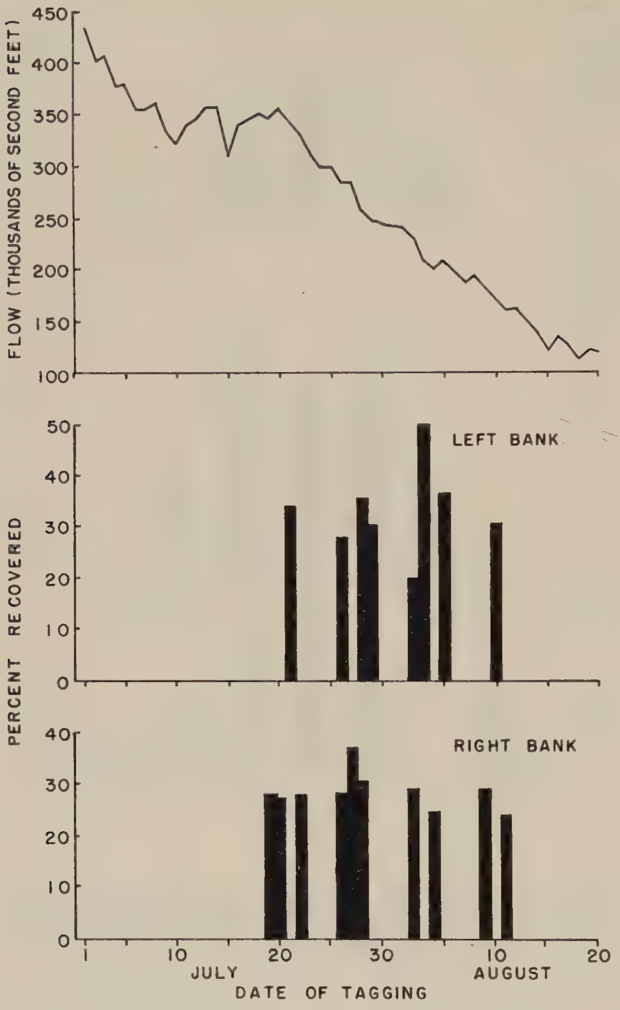


FIGURE 10.—Recoveries of tagged sockeye upstream expressed as percentages of the number tagged at each bank below, compared with water flow, 1955.

TABLE 11.—*Returns at Rock Island Dam and upstream of different kinds of tags used*

Year and kind of tag	Tagged	Returns at Rock Island		Tagged[2]	Returns upstream	
		Observed [1]			Recovered	
1954	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
Bar	1,284	1,121	87.3	1,260	320	25.4
Spaghetti	565	241	42.7	556	155	27.9
1955 [3]						
Bar	1,174	855	72.8	1,000	317	31.7
Spaghetti	310	123	39.7	179	50	27.9
1956						
Bar	770	671	87.1	764	197	25.8
Streamer	509	423	83.1	506	128	25.3

[1] Undetermined tag observations at Rock Island not identified as bar, spaghetti, or streamer are omitted.

[2] Steelhead and those tagged fish removed at Rock Island for other experiments were omitted from this column.

[3] Only sockeye are included in the upstream returns in 1955 because of the unequal recovery effort spent on chinooks tagged with the two kinds of tags.

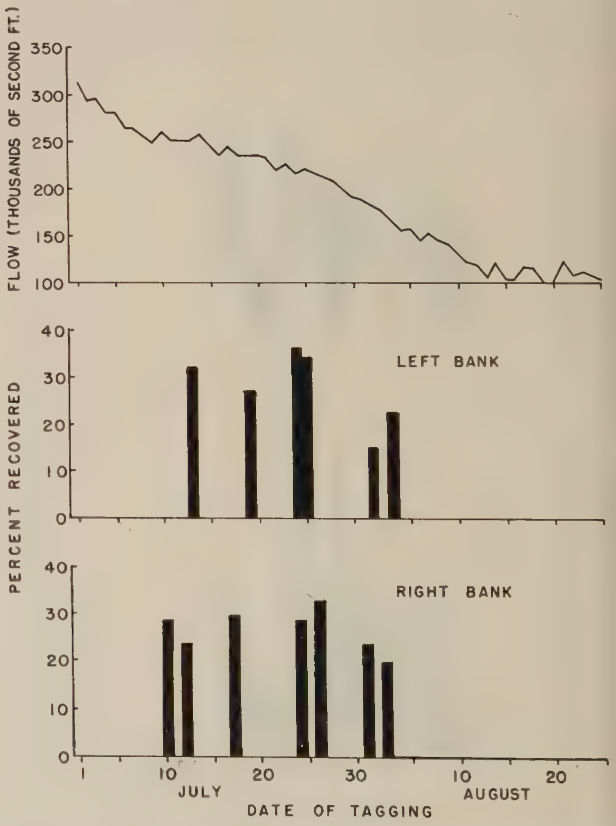


FIGURE 11.—Recoveries of tagged sockeye upstream expressed as percentages of the number tagged at each bank below, compared with water flow, 1956.

Table 12.—*Returns of tagged fish at Rock Island Dam by ladder, 1953–56*

Year	Tagged below Rock Island[1]	Observations by ladder						Total tag observations	
		Left		Center		Right			
	Number	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1953	764	298	39.0	87	11.4	106	13.9	491	64.3
1954	1,849	788	42.6	399	21.6	188	10.2	1,375	74.4
1955	1,484	656	44.2	205	13.8	127	8.6	988	66.6
1956	1,279	724	56.6	214	16.7	156	12.2	1,094	85.5
Total	5,376	2,466	45.9	905	16.8	577	10.7	3,948	73.4

[1] Tagged members included chinook, sockeye, and steelhead.

Rock Island Dam. An illustration was the Bonneville experiment (app. p. 366) where a distinctive copper and black disk tag was used; only 6 of these tags were reported at Rock Island, but 14 were recovered upstream. In view of these examples, it was undoubtedly true that the counters missed tagged fish.

Tagging operations have caused mortalities. Schaefer (1951) concluded that there was a serious differential mortality among the tagged and untagged fish during the long migration between the Harrison trap and the Birkenhead River. Nelson[1] found a differential mortality between tagged and untagged sockeye migrating between Karluk River weir and weirs on the tributary spawning streams of Karluk Lake.

The loss of tags from tagged fish apparently was not a reason for the missing tags at Rock Island Dam. No tag-scarred salmon were reported by the counters at Rock Island Dam, and neither were any caught in the traps, though many tagged fish were captured there.

Tagged salmon may have refused to reenter the fishways after tagging. In 1956, five tagged salmon were observed in the Oregon Fish Commission's trap at McNary Dam, located approximately 160 river-miles downstream from Rock Island Dam. Also, a tagged sockeye was observed at the Redfish Lake weir in Idaho, about 700 river-miles from Rock Island Dam. Howard (1948) reported that handling during tagging operations at Cultus Lake, British Columbia, apparently caused some of the tagged sockeye to remain in the area immediately above the tagging location, rather than continue their migration. Undoubtedly some of the missing tags at Rock Island Dam could be attributed to straying.

Finally, mortalities could be caused by the dam. Mortalities were indicated for some experiments but not for others when comparing upstream recovery ratios from tagged fish released above and below the dam.

Returns by area of release.—The results of tag returns by ladder are shown in table 13. These data show a consistent pattern of passage over the ladders for the 3 years and for the two release areas. Only 6 to 12 percent of the fish used the right ladder.

The observed differences in returns from the two banks over the 3 years would indicate that right bank tag releases were not as successful in passing the dam as left bank releases.

Table 13.—*Tag returns by area of release and ladder, 1954–56*

Year and release area	Tagged	Observations by ladder[1]							
		Left		Center		Right		All ladders	
	Number	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1954									
Right bank	950	389	40.9	192	20.2	80	8.4	661	69.6
Left bank	899	352	39.2	187	20.8	92	10.2	631	70.2
1955									
Right bank	793	311	39.2	91	11.5	47	5.9	449	56.6
Left bank	691	302	43.7	104	15.1	70	10.1	476	68.9
1956									
Right bank	616	331	53.7	94	15.3	76	12.3	501	81.3
Left bank	663	385	58.1	119	17.9	77	11.6	581	87.6

[1] Unidentifiable tags were excluded.

Since almost all of the fish were trapped in the left ladder or in the forebay trap at the head of this ladder, and since they were released at both banks below the dam, it was important to know whether these fish had learned the route for their second passage of the dam. Accordingly, the tag returns were listed by trapping site and by area of release (table 14). Regardless of where the fish were trapped or released, they returned in approximately the same ratio over the three ladders with the least returns always at the right ladder. It is evident that the salmon did not learn a route and then repeat this route for a second passage over the dam. Neither were they necessarily frightened away from a ladder, since the majority of fish returned to the left ladder, where most were trapped previously.

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[1] Nelson, Philip R., unpublished data 1947 and 1948. U.S. Fish and Wildlife Service, Seattle, Wash.

TABLE 14.—*Tag returns by ladder of salmon trapped at both ladders and released at both banks below Rock Island Dam, 1954–55*

Year and trapping area	Area released	Tagged	Observations by ladder [1]					
			Left		Center		Right	
		Number	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1954								
Right ladder	Right bank	178	56	64.4	20	23.0	11	12.6
Left ladder	Right bank	748	331	57.9	172	30.1	69	12.1
Left ladder	Left bank	923	354	55.9	187	29.5	92	14.5
1955								
Right ladder	Right bank	363	169	72.5	49	21.0	15	6.4
Left ladder	Right bank	430	142	65.7	42	19.4	32	14.8
Left ladder	Left bank	691	302	63.4	104	21.8	70	14.7

[1] The percentage by ladder is based on total observations.

Tagged and untagged fish movements.—Table 15 shows the comparison of choice of ladders between tagged and untagged salmon for each season of tagging. Chinooks and sockeye were combined because of the error of confusing chinooks (jacks) with the sockeye. The percentage returns at the right ladder agreed closely with those of the untagged run. A somewhat larger proportion of the untagged run, compared with the tagged fish, chose the left ladder for passage. The percentage returns at the middle ladder were greater than the proportion of untagged fish at this ladder. This may be because right bank releases, failing to enter the right ladder, were attracted by the center ladder before the left ladder. Generally speaking, however, the tagged and untagged salmon were similar in their patterns of passage.

During the years of the tagging experiments, the four spillway regulating gates nearest the right ladder were kept closed so the high-velocity flows would not interfere with fish approaching along the right bank. In 1957, in order to test their influence on fish passage, these gates (one or more) were opened when most of the fish passed the dam. The percentage of chinooks and sockeye using this ladder in 1957 increased to 24 percent, compared to an average of 15 percent for 1953–56. This was the pattern of fish passage at the right ladder by species—chinooks, 19.8 percent; sockeye, 26.8 percent; and steelhead, 16.6 percent. No tagging was done in 1957, and a comparison of tagged fish movements could not be made. Apparently the salmons' choice of ladders can be influenced by manipulating the regulating gates and by the resulting changes in flow patterns below the dam.

TABLE 15.—Combined chinook and sockeye counts of the tag returns and the untagged runs by ladder, 1954–56

Year	Combined chinook and sockeye counts						Total
	Left ladder		Center ladder		Right ladder		
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*
1954							
Tagged	787	57.3	399	29.0	188	13.7	1,374
Untagged	86.439	70.0	17,144	13.9	19,892	16.1	123.475
1955							
Tagged	654	66.3	205	20.8	127	12.9	985
Untagged	139,555	77.4	22.415	12.4	18,448	10.2	180.418
1956							
Tagged	724	66.2	214	19.6	156	14.2	1,094
Untagged	88,154	75.0	18,697	15.9	10,677	9.1	117.528
Total 1954–1956:							
Tagged	2,165	62.7	818	23.7	471	13.6	3,454
Untagged	314,148	74.5	58,256	13.8	49,017	11.6	421,421

DETERMINATION OF DELAY AT ROCK ISLAND

In this paper delay means the period of time that Rock Island Dam checks the migration of salmon under present conditions.[2] Delay may cause salmon mortalities prior to spawning. Some causes of delay may be flood waters in rivers, low flows, high water temperatures, areas of difficult passage (as in precipitous canyons), or dams in rivers. Delay here is measured as days elapsing between release of tagged fish and subsequent observations at the counting boards. The delay also is assessed by comparing, at upstream points, the time of arrival of tagged fish released above and below the dam. The difference in time of arrival at an upriver point would be a measure of delay at the dam, and this difference should correspond to the delay observed at Rock Island Dam. It will be shown that this was true.

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[2] An argument advanced is that studies of delays at dams should consider comparisons of travel rates before and after a dam is built. This has seldom been accomplished; subsequent to this study, comparisons of travel rates were made before and after Rocky Reach dam was built. Major, Richard L. and James L. Mighell. A study to measure delay to upstream migrating salmonids at Rocky Reach Dam. Manuscript. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

RETURNS FROM UPSTREAM

Sockeye Salmon

It was necessary that days-out of tagged fish at upstream points be measured at a point where a minimum of mixing of (1) chronological order of movement and (2) delay might occur. Zosel Dam, on the Okanogan River, approximately 145 river miles above Rock Island Dam, appeared the best place for measuring the period of migration of tagged sockeye salmon. The sockeye passing this dam were headed for Lake Osoyoos and the spawning areas above the lake. They passed the dam easily, either through fishways or through the spillway. Unfortunately, not many tagged fish were released in the forebay at Rock Island in 1954, the year many sockeye and tags were observed at Zosel Dam. In 1955 and 1956, larger samples were released above the dam at Rock Island but most fish passed Zosel Dam unobserved. These data, at Zosel Dam, however, did allow us to compare the migration period of different lots of tagged fish.

Tumwater Dam on the Wenatchee River, the only other fish-passage observation point, presented a delay and mixing problem which precluded a reliable comparison of time periods for different tagged lots. At this dam, all fish had to find and ascend the ladder to pass the dam, and this offered chances for mixing and delaying of various parts of the salmon runs. The data obtained at Tumwater Dam are given for comparative purposes.

Figure 12 shows the days-out period at Zosel Dam for sockeye released at three areas at Rock Island. Looking at the modal values, we note a 2-day difference between forebay and left bank below the dam releases for both 1954 and 1955. The right bank modes, however, show a 3-day difference for 1954 and a 4-day difference for 1955. This would indicate right bank releases were delayed longer than left bank releases. The mean values do not indicate this difference between banks. Since the means are influenced by extreme values, however, the modal values should be preferred when making comparisons, provided the data are sufficient for forming smooth distribution curves. The number of observations leave something to be desired, but they indicate a delay of from 2 to 4 days at Rock Island, and a greater delay for right bank releases than left bank releases below the dam.

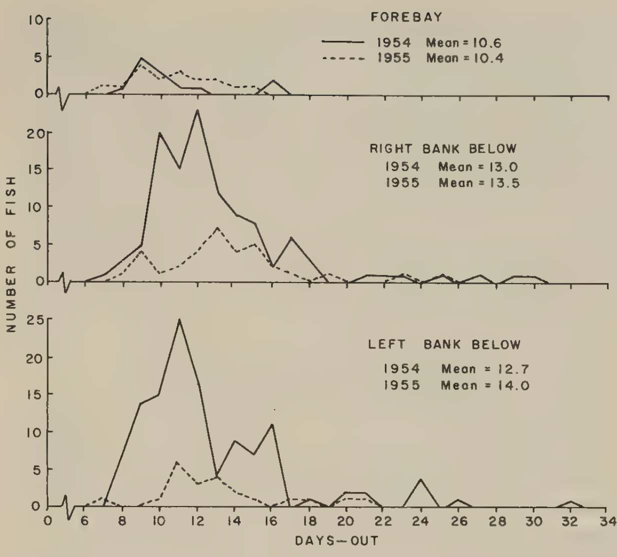

FIGURE 12.—Number of days out at Zosel Dam of tagged sockeye released at three different areas at Rock Island, 1954–55.

At Tumwater Dam, the difference in days-out between above- and below-dam experiments averaged 2 to 3 days in 1954 and 1955 (table 16). We observed that for these 2 years right bank releases took longer to pass than left bank releases. The 1956 results may have been affected by changed flow patterns at Tumwater Dam, the entire river was spilled over the dam and no water was diverted for power production as in previous seasons. The great range in individual days-out of tagged sockeye is indicated by the large standard deviations shown for the data.

Chinook

Our only upstream measure of the days-out period of tagged chinook salmon was obtained at Tumwater Dam. All other tag recoveries were from the spawning grounds or hatcheries,

TABLE 16.—*Means and standard deviations of days-out at Tumwater Dam of tagged sockeye released at different areas at Rock Island Dam, 1954–56.*

[Figures in parentheses are standard deviations]

Year	Release area at Rock Island Dam				Difference between above and total below
	Left bank below	Right bank below	Total below	Above dam	
1954	23.5 (7.3)	24.7 (7.0)	23.9 (7.2)	20.8 (5.9)	3.1
1955	21.6 (7.5)	22.1 (7.1)	21.8 (7.3)	19.9 (8.2)	1.9
1956	21.5 (8.0)	21.5 (9.4)	21.5 (8.4)	20.3 (7.9)	1.2

where the chronological order of the arrival of tagged fish could not be determined. At Tumwater Dam, moreover, migrating chinooks were subject to delay, and conclusive data of the time-out period for fish from the different tagging areas were not obtained. The days-out at Tumwater Dam for individual chinooks ranged from 11 to 65 days, and there was no evidence that any one group of releases was different from another group.

RETURNS AT ROCK ISLAND

Sockeye

As hypothesized previously, the difference in days-out at upstream points between above- and below-dam releases should equal the days-out period at Rock Island Dam of below-dam releases. The results at Rock Island Dam (fig. 13) confirm the hypothesis. The majority of fish passed through the fishways within 2 to 4 days after being released below the dam. In 1953, the peak of the days-out curve occurred a day earlier than in 1954-56. This may have been because the majority of fish in 1953 were tagged during a 3-day period near the end of the run in contrast to the season-long tagging of the later years.

The comparisons of days-out by area of release at Rock Island are shown in figures 14, 15, and 16. At first glance we have a fairly consistent picture of passage from the two areas of release, with the exception of the right bank releases in 1956. A better comparison of the days-out period for each release area is gained from the following array of modal values of days-out for each tag release area and the ladder of passage (table 17).

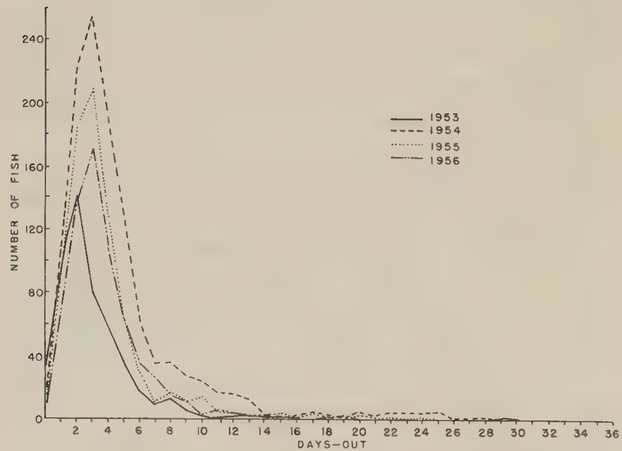

FIGURE 13.—Comparison of days-out at Rock Island of tagged sockeye released below the dam, 1953–56.

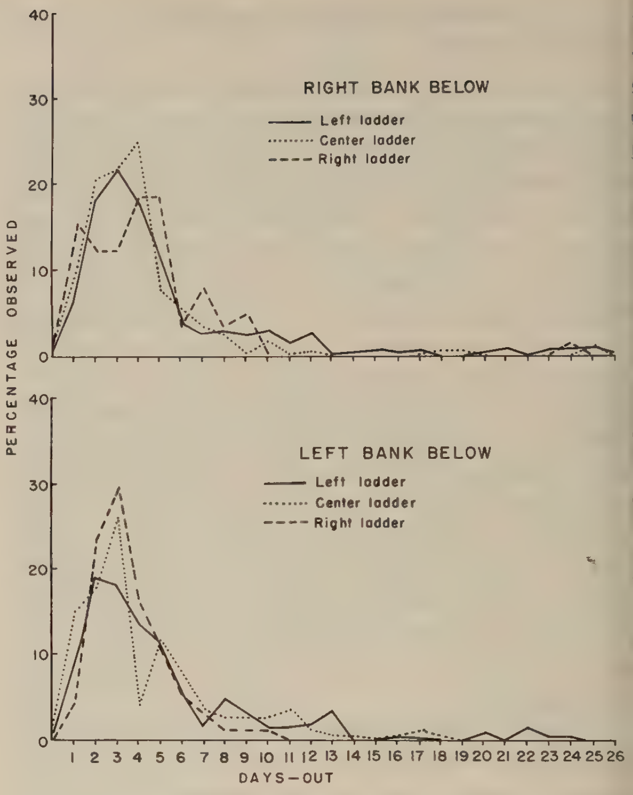

FIGURE 14.—Days-out of tagged sockeye at Rock Island for each area of release expressed in percentages of total observations by ladder, 1954.

In 1954, right bank releases took a day longer to pass at each ladder than the left bank tag releases. This difference was not noted for other years except in 1955, in the center ladder. In 1956, right bank releases passed sooner than left bank releases. The 1956 tagged fish, it is recalled, were released off the face of the dam close to the fishways. Apparently the few sockeye using the right ladder moved into the ladder immediately after tagging and the remainder moved downstream or across the river. Those sockeye using the right ladder possibly moved up sooner upon finding the ladder because of the absence of resting areas below the ladder.

Measuring the number of days-out for tagged salmon at Rock Island Dam depended on the ability of the counters to distinguish the kinds and colors of tags used. As previously pointed out, the counters made many errors. To test if the counters were approximately correct in identifying most tags upon which the days-out data were derived, the occurrence of tagged salmon, regardless of tag color or kind, was plotted by date and compared with the total number of salmon tagged (fig. 17). An examination of the graphs reveals that the peaks and troughs of the tag occurrence curve occur 2 to 4 days after the start and finish of a tagging period. This 2- to 4-day lag compares with the days-out curve of figure 13 and indicates the counters were approximately correct in identifying most of the tags from which the days-out data were derived.

Table 17.—*Modal values in days out for each tag release area and ladder of passage*

[Data from figs. 14, 15, and 16]

Releases	Ladder		
	Left	Center	Right
1954			
Left bank	2	3	3
Right bank	3	4	4–5
1955			
Left bank	3	2	2
Right bank	2	3	2
1956			
Left bank	3	2	3
Right bank	3	2	1

Undoubtedly the difference in time required for salmon released above and below Rock Island Dam to reach an upstream point reflects the amount of time required for the below-dam releases to pass the dam. Thus, it is reasonable to conclude that tagged sockeye were delayed 2 to 4 days below Rock Island Dam. Assuming that tagged and untagged salmon migrate at similar rates, Rock Island Dam delays sockeye approximately 2 to 4 days.

Chinook

At Rock Island Dam spring chinook peaked after 1 day-out and summer chinook on the third

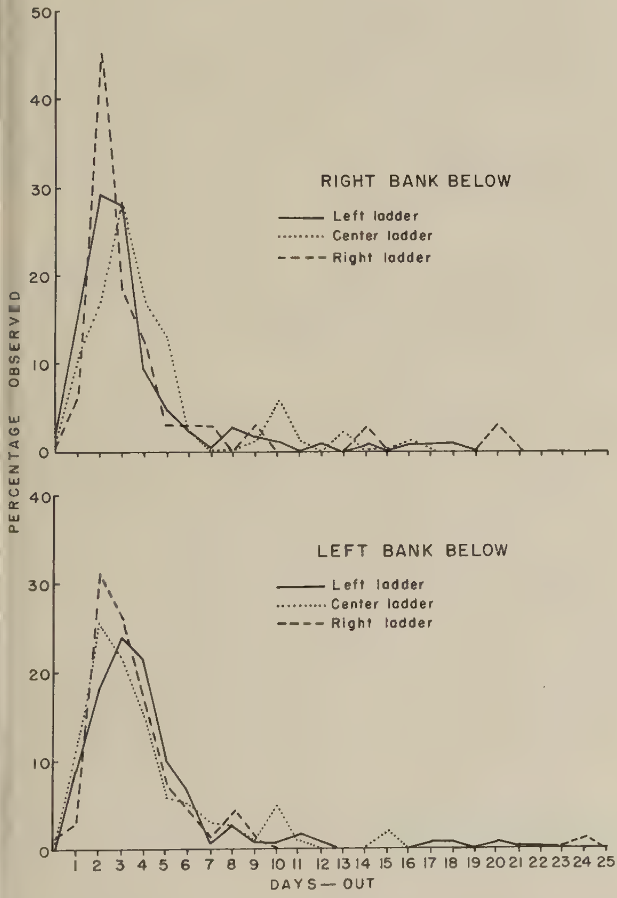

Figure 15.—Days-out of tagged sockeye at Rock Island for each area of release, expressed in percentages of total observations by ladder, 1955.

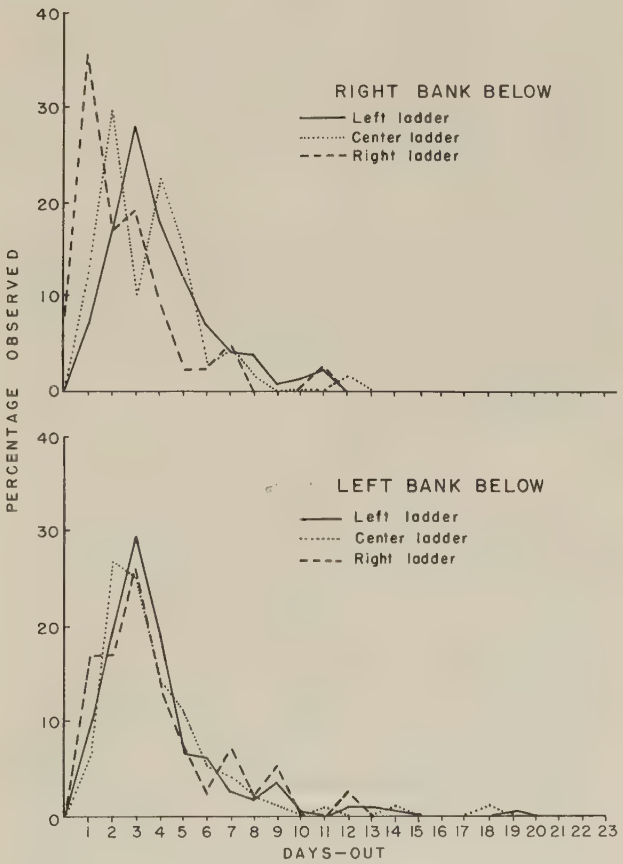

Figure 16.—Days-out of tagged sockeye at Rock Island for each area of release, expressed in percentages of total observations by ladder, 1956.

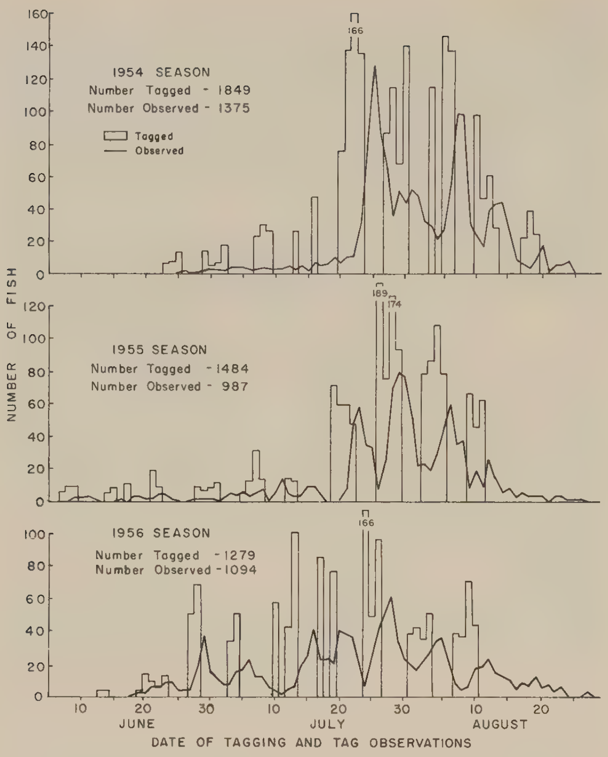

FIGURE 17.—Numbers of salmon tagged below Rock Island, and numbers of daily tag observations at the counting stations.

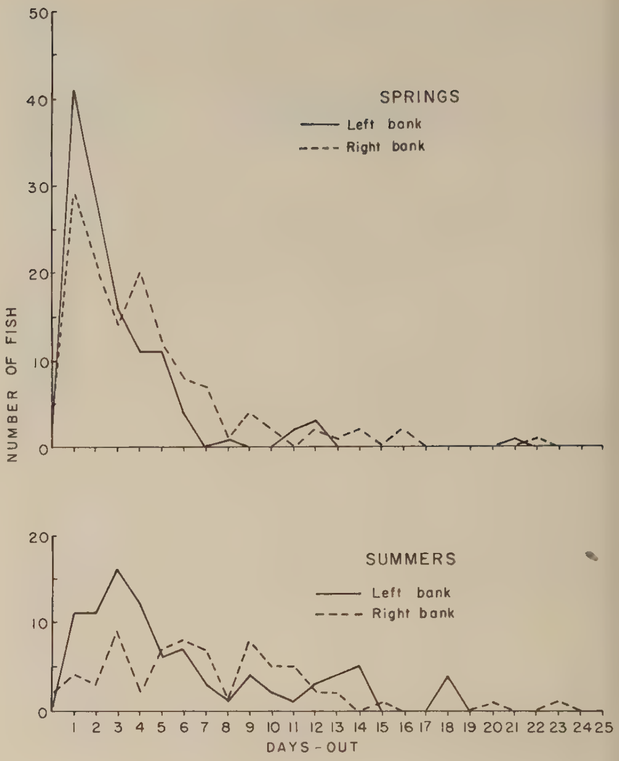

FIGURE 18.—Comparison of days-out at Rock Island of tagged spring and summer run chinook, by area of release, 1956 season.

day after tagging (fig. 18). The drawn-out time period noted for many summer chinooks may have resulted from errors in species identification as this run coincides with sockeye, or it may be characteristic of the summer chinook to take longer to pass the dam.

DISCUSSION

EXPERIMENTAL SITUATION

In view of conflicting results for different years and for different tagging areas, it is pertinent to review briefly the experimental situation and sources of error of the tagging experiments.

We have assumed that the likelihood of recovering or observing a tagged fish in a given recovery area was the same regardless of the area of release or time of tagging. This seems a reasonable assumption, because recovery efforts on spawning grounds were directed to all parts of the spawning areas and throughout the period of spawning. Tagged fish also were recorded as they passed Zosel Dam on the way to the spawning grounds, although sockeye could pass Zosel Dam without passing through counting traps. At Tumwater Dam, all fish, in order to pass the dam, had to pass through a trap where tagged fish were easily observed and counted.

We have assumed also that proportions of tagged fish migrating to different spawning areas were the same for the different release lots. In sampling fish for tagging, salmon were trapped throughout the duration of the run and usually during the height of the daily migration. In many instances, individual truck loads of fish were divided between above-dam and below-dam taggings. Other times, successive loads of fish were divided between left and right bank releases and above and below-dam releases. On this basis we feel that the above assumption is reasonable.

Another factor relating to experimental control was the kind of tag used for the various experiments. All the fish released above the dam were tagged with paired plastic disks. Different color combinations or single colors were used for different release groups. Tags used on fish released below the dam consisted of disks of single colors in combination with plastic bars, nylon streamers, or vinyl tubing (spaghetti). Tags used below the dam were larger than the tags used above the dam. It might be argued that a larger, different shaped tag would aid recovery or observation of a tagged fish released below the dam. In considering the conditions for tag recoveries and observations, we do not agree with this argument. At Tumwater Dam all tags were observed in clear water from a distance of 3 or 4 feet. Most tags were read for numbers; thus, differentiation of tags from above and below the dam should have been readily apparent. This also holds true for tag observations at Zosel Dam. On the Okanogan River spawning grounds, tags were recovered from dead spawned-out fish or were observed during surveys of the river. In the latter case, biologists identified tags from 5 to 25 feet away and recognition was easy. In fact, when viewing tagged fish from the Tumwater Dam suspension bridge and from the railroad bridge just below Zosel Dam, both suspended 20 to 30 feet above the water, we could easily discern sizes and shapes of tags. Biologists observing fish at Rock Island distinguished, from about 40 feet away, shapes, sizes, and colors of tags on fish in the tailrace just below the fishway.

So far as tag colors are concerned, all tags used below the dam had single-colored disks and single-colored bars, streamers, or spaghetti. Tags used above the dam had single or bicolored patterns on the disks. It is difficult to say what the differences in colors or color combinations mean in terms of likelihood of recovery. Based on our observations of hundreds of tags under many circumstances, we believe that the tags, when seen, can be differentiated by color and kind.

ALTERNATIVE MODELS FOR ESTIMATING MORTALITY

Several models were considered for estimating mortalities in addition to the one used (ratios of recovery proportions of tagged fish from different release areas). We were unable, however, to accept the assumptions necessary for some. In others, dubious and conflicting results were obtained; hence, they are not given in detail in this paper. Two models are discussed briefly.

In one model we determined the racial composition of sockeye salmon in the tagged sample by estimating the number of 4-year-old upriver fish from the relative abundance of 3-year-old Okanogan fish in the tagged lots, and using the ratio of fishway counts to numbers released, as an adjustment factor in estimating the relative abundance of Wenatchee tagged fish in different release groups. Another model estimated racial composition from the differences in the proportions of 3-year-old sockeye in the populations at Rock Island Dam and in the Okanogan River, caused by a segment of the 4-year-old sockeye population splitting off and entering the Wenatchee system. In neither of these two models were definitive results obtained regarding mortalities caused by the dam. Mortalities were indicated for some years and areas, not for others. Because of these conflicting and nondefinitive results, we feel the best approach to the problem is that given.

MORTALITIES

Populations of anadromous salmonids lose some members passing large dams. For years, dead salmon have been observed floating down the Columbia River below Bonneville Dam, apparently fish which failed to pass the dam. Using the results of experiments involving the marking and recovery of dead salmon carcasses, Merrell and Collins [3] estimated a salmon loss at Bonneville Dam. Thompson (1945) found that a serious decline in Fraser River sockeye salmon runs was related to an area of difficult passage and to an obstruction in the river, even though salmon were known to pass this area each season. In a later paper on the Fraser River sockeye salmon, Talbot (1950) found that fish delayed longer than 14 days at Hells Gate did not reach their spawning grounds.

The tagging experiments at Rock Island gave conflicting results of mortalities caused by the dam. We found no mortalities for 3-year-old sockeye salmon when comparing recoveries of tagged fish released above and below the dam. We found mortalities in many experiments for 4-year-old sockeye when comparing tag returns from above and below dam releases. In other experiments involving these 4-year-old fish, no mortalities were indicated. Most experiments with chinook salmon indicated no mortalities caused by the dam.

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[3] Merrell, Theodore R., and Melvin D. Collins. An investigation of adult chinook salmon mortality in the vicinity of Bonneville Dam, 1954 and 1955, on the Columbia River. Fish Commission of Oregon, August, 1960. 150 p. (Contract No. DA-35-026-eng-20892, U.S. Department of Interior, Fish and Wildlife Service.)

Results show that mortalities caused by the dam are neither substantial nor consistent over the years, or that our tagging methods could not detect mortalities accurately. Confidence limits for the point estimates of mortalities ranged from zero (in many instances) to about 28 percent for the lower limits; upper limits ranged from 20 to 66 percent.

Comparatively few tagged fish used the right ladder (also observed for untagged runs), even when they were released near it. Apparently, the majority of these salmon ascended other ladders. An increased percentage of the salmon was attracted to the right ladder in 1957 when spillway gates on the right side of the dam were opened during the fish migration season. Previously these were closed to reduce water turbulence near the right ladder entrance. It may be that the added flow attracts fish to this bank and into the fishway.

While altering the right bank fishway might induce more fish to use the right ladder, we cannot say it would result in markedly improved facilities with respect to mortalities.

DELAY

Delay of migrating adult salmon runs is very important to the survival of the runs. As Thompson (1945) and Talbot (1950) pointed out, delays to sockeye salmon runs in the Fraser River caused mortalities and a serious decline in the runs. Schoning and Johnson (1956), in a study at Bonneville Dam on the lower Columbia River, reported that migrating chinook salmon were delayed 2.6 to 3 days. The 2- to 4-day delay at Rock Island Dam may not be important in itself, but if the delay is multiplied by a series of dams, serious losses of anadromous fish populations may result.

We do not know if upper river salmon runs would survive the series of delays in migration that may result when all Columbia River dams are completed. It may be that delays, if short-termed would be compensated for by easier and faster travel through the reservoirs created by the dams. These salmon do not spawn immediately upon reaching the spawning areas. There is an interval before spawning, of from 1½ to 2½ months after the salmon pass Rock Island Dam. This ripening period has been noted on other river systems. Howard (1948) found that the period for sockeye in Cultus Lake, British Columbia was about 1 month. Schaefer (1951) noted the time for sockeye in the Harrison River system of British Columbia, was a month or less. The ripening period for sockeye in Lakelse Lake, British Columbia, averaged 54 days (Fisheries Research Board of Canada, 1954). In the Bristol Bay area of Alaska, some sockeye remain in the lakes up to 3 months before spawning. The ripening period evidently is a necessary adjunct to the migration time.

In this study at Rock Island Dam, we discovered a 2- to 4-day delay to migrating salmon. Upstream tag observations at Zosel Dam indicated that fish tagged and released below the right ladder were delayed longer than fish tagged and released below the left ladder. This was confirmed by comparing returns of left and right bank tag releases at Rock Island for 1954. The longer delay was absent in 1955 and 1956. Thus, while we do not have positive evidence of a greater delay for fish released below the right ladder, such a delay is indicated.

Altering the right-bank fishway may lessen delay at the dam because of the possible increased chances of salmon finding a ladder sooner. However, the same delay pattern was noted at Bonneville Dam (app.), where ladders at both sides of the dam were designed to be equally attractive. From this study, we cannot conclude that altering the right bank fishway would decrease materially the overall delay at Rock Island Dam.

SUMMARY AND CONCLUSIONS

We conducted a tagging program at Rock Island Dam during 1953–56 to determine whether the dam caused loss or delay of salmon passing the dam, and whether such loss or delay was associated with the failure of fish to find and use the dam's right bank fishway. In this study, tagged salmon were released below the left and right bank fishways and above the dam. Fish counters at the dam identified different tag groups by noting the different colors and kinds of tags on salmon crossing the counting boards. Tags also were identified at upstream points on migration routes and during spawning surveys.

A comparison of upstream tag recoveries from the different release areas gave conflicting results regarding losses of fish. Point estimates of losses, for some combinations of years and release areas (left or right bank below the dam), ranged from 0 to 42 percent, with mortalities greatest for fish released below the right bank ladder. Tagging data on chinook salmon indicated a loss of spring chinooks released below the right ladder in 1956; no loss was indicated, however, in comparing total returns from below the dam with returns from above the dam. For summer chinooks, tagging data failed to show losses due to the dam.

Total tag returns at Rock Island Dam, as identified by fish counters, ranged from 64 to 86 percent of the number released below the dam during the experiments. Straying and mortalities may have accounted for many of the missing tags; it was probable also that the counters missed many of the tags, and total returns were greater than indicated.

Tag returns at Rock Island Dam from below-dam releases showed that although salmon were released at both banks, the majority returned over the left ladder. Only 12 to 14 percent of the tagged salmon returned over the right ladder. The tag returns corresponded closely with the choice of ladders of the untagged populations, of which the majority chose the left ladder for passage and 10 to 17 percent the right ladder. Although the salmon were taken from the ladders for tagging, they did not learn a particlar route in re-passing the dam; neither were they frightened from a particular ladder during repassage of the dam.

Tagged salmon released above Rock Island Dam arrived at upstream points 2 to 4 days earlier than fish released below the dam. This difference in days out corresponded to the time required for most fish to pass Rock Island Dam after tagging, and is termed the delay at the dam. Fish released below the right ladder apparently were delayed 1 to 2 days longer in reaching upriver points than fish released below the left ladder.

The days-out period at Rock Island Dam, for sockeye released at the two banks below the dam, was essentially the same, with most of the salmon passing in 2 to 4 days, and the peak occurring the third day after tagging. In 1954, right-bank releases were delayed 1 day longer than left-bank releases. This greater delay of right-bank releases was not evident in 1955 and 1956. Spring chinook peaked after 1 day-out, with the majority passing the dam by the fourth day. The peak day for summer chinook was the third day after tagging. No apparent difference in days-out period at Rock Island Dam was indicated for chinooks released at the two banks below the dam.

An increased percentage of the run used the right ladder in 1957, following a change in spillway-gate operating procedures. Evidently attraction to this ladder was increased by opening gates on the right side of the dam next to the fishway.

On the basis of these tagging studies we found that Rock Island Dam delayed migrating salmon from 2 to 4 days. There is conflicting evidence of a greater delay to fish released below the right ladder than to fish released below the left ladder. Data regarding mortalities gave conflicting results; some experiments indicated substantial mortalities while others indicated none. While altering the right-bank fishway may attract more fish to the fishway, we cannot say it will necessarily improve passage considering overall loss and delay. The delay of 2 to 4 days may be significant when similar delays at a series of dams are considered.

ACKNOWLEDGMENTS

Many persons in addition to staff members at the Seattle Biological Laboratory contributed to the tagging experiments at Rock Island Dam. The Washington State Department of Fisheries helped in planning the project, and provided equipment for the investigations. The Puget Sound Power and Light Company, and Chelan County Public Utility District No. 1 gave valuable assistance by providing equipment and facilities. R. A. Fredin and D. D. Worlund of the Bureau's Biological Laboratory in Seattle assisted with the statistical analyses.

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APPENDIX

BONNEVILLE TAGGING EXPERIMENTS

At the conclusion of the Rock Island tagging experiments in 1954, we were confronted with the apparent loss at the dam of many tagged fish. What was the meaning of observing only approximately 75 percent of the tags released below the dam in 1954 and 64 percent in 1953? In the following years, 65 percent in 1955 and 86 percent in 1956 of all tags released were subsequently recorded by fish counters. Were these percentage returns due to conditions associated with the Rock Island fishways or could low percentage returns from tagging be expected at any dam? In an attempt to answer these questions we decided to tag, on a small scale, below another dam in the same manner as at Rock Island. The objectives were to determine the percentage and pattern of tag returns at Bonneville Dam and compare them with the Rock Island tagging data.

On July 14 and 15, 1955, 293 fish were tagged and released below Bonneville Dam located on the Columbia River approximately 140 miles above the river's mouth. The procedure at Bonneville was the same as at Rock Island. Fish were trapped in a ladder, transported by truck, and tagged and released below the dam. The experiments differed somewhat from those at Rock Island in that the fish were released about one mile below Bonneville on only one bank while at Rock Island they were released about 1,000 feet below the dam at both banks. Also, fish at Bonneville were tagged with paired disks and not the combination tags applied at Rock Island.

Table A–1.—*Returns at Bonneville Dam of tagged salmon and steelhead released below the dam in 1955*

Species	Tagged	Returns by ladder			Returns No. tagged
		Washington shore	Bradford Island	Total	
	Number	*Number*	*Number*	*Number*	*Percent*
Sockeye	160	47	25	72	45.0
Chinook	17	9	30	[1] 39	229.4
Steelhead	116	36	16	52	44.8
Totals	293	92	71	163	
Percent by ladder		31.4	24.2	55.6	

[1] This is an obvious error in species identification.

Tag Returns at Bonneville

The number tagged and the returns at Bonneville are shown in table A–1. Far more steelhead were tagged at Bonneville than during the Rock Island experiments. Tag returns of 55.6 percent reported over Bonneville Dam by the fish counters were less than for any season at Rock Island, where percent returns ranged from 64 to 86 for the seasons 1953–56. Nine tags were returned from below Bonneville, six from dead fish found on the beaches and three from fishermen. At Rock Island the largest number of recoveries from below the dam occurred in 1956 when seven were recovered. Of these, five were from McNary Dam where a trap was installed for other tagging projects, one was returned by a sports fisherman, and one was observed in Redfish Lake in the Snake River system.

One feature found at Bonneville and not at Rock Island is the ship locks through which it is possible for fish to pass. There was no way of knowing whether or not any tagged fish passed the dam by this means.

As at Rock Island, the returns indicated fish counters had trouble identifying species. This is evident when 39 tagged chinook were reported by the counters and only 17 had been tagged. This same kind of error was noted at McNary Dam where fish counters reported 23 tagged chinooks from this same experiment.

The time-out period (time elapsing between tagging and observation at the counting boards) for tagged fish at Bonneville was similar to results obtained at Rock Island. Figure A–1 shows the number of days-out for all tagged fish observed at Bonneville. The majority of the fish passed in 2 to 5 days after tagging. There is an inherent error in the figure because days-out were computed from July 14, the first day of tagging, although half the fish were tagged on July 15. There was no way for the counters to distinguish between the two lots. Correctly then, many fish passed 1 day sooner than indicated. It is notable that these results are similar to those from the Rock Island experiments in which the majority of fish passed in 2 to 4 days.

Figure A–2 shows the days-out by ladder at Bonneville. Many fish (44 percent) crossed the river to pass upstream through the Bradford Island ladder, although the fish were trapped and released on the Washington shore. The mean days-out time for fish passing through the two ladders was approximately the same: 6.6 days for the Washington shore ladder and 6.8 days for the Bradford Island ladder. Again, these results were similar to those obtained at Rock Island.

Tag Returns—Bonneville to McNary Dam

Tag recoveries were obtained above Bonneville Dam from the commercial fishery, sports fishermen, the Celilo Falls fishery, at McNary Dam, at Rock Island Dam, and also from spawning ground surveys above Rock Island. For the area between Bonneville and McNary Dams, 28 sockeye and 3 steelhead tags were returned by commercial fishermen and the Indian dip net fishery at Celilo Falls. Sports fishermen fishing in the various tributaries returned tags from seven tagged steelhead.

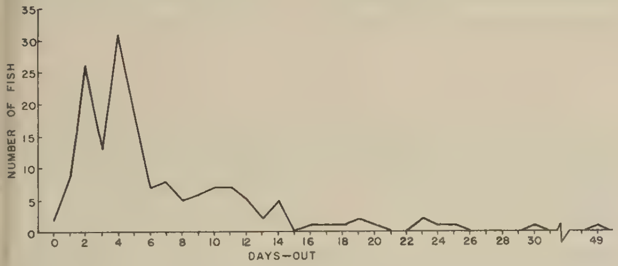

Figure A–1.—Number of days-out at Bonneville of tagged fish released below the dam, 1955 season (days-out dated from July 14).

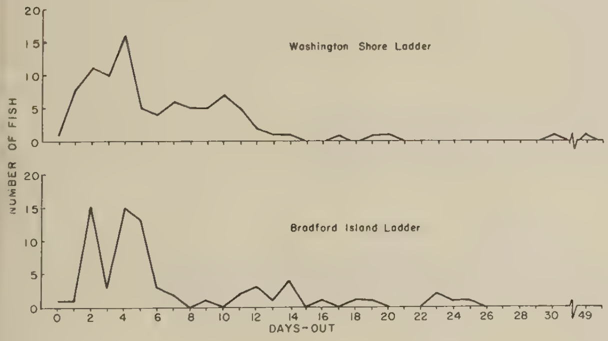

Figure A–2.—Number of days-out by ladder at Bonneville of tagged fish released below the dam in 1955 (days-out dated from July 14).

At McNary Dam, approximately 120 miles above Bonneville, 84 of the Bonneville tagged fish were recorded at counting stations. This was 28.7 percent of the number tagged and 51.5 percent of the number recorded over Bonneville Dam. The total number of tags accounted for from Bonneville to and including McNary counts was 122, or 41.6 percent of the number tagged and 74.8 percent of the number reported over Bonneville.

Figure A–3 shows the days-out for tagged fish at McNary Dam. The double mode is pronounced for each species and the modes are 5 days apart for chinooks and sockeye. It is doubtful that the 5-day interval is the result of computing days out from the first day of tagging when tagging occurred on 2 successive days. It is more likely that some short-term delay affected a group of fish, possibly those tagged the second day. The figure shows that the majority of tagged fish took from 12 to 20 days to pass McNary Dam after being tagged below Bonneville Dam.

Tag Returns Above McNary Dam

The Rock Island fish counters were alerted to the particular tag applied at Bonneville and recorded its appearance on fish. The tags used were paired disks of a copper color with a black bullseye, a very distinctive color, and much

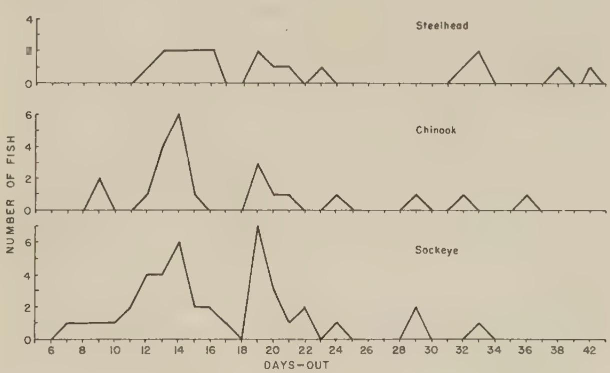

Figure A–3.—Number of days-out at McNary Dam for the three species tagged below Bonneville Dam in 1955 (days-out dated from July 14).

different from the tag combinations used below Rock Island. The counters reported five sockeye and one chinook tag of this group between August 3 and August 21. However, the counters were apparently unable to observe and identify this particular tag easily, for 14 tags (11 sockeye, 2 chinooks, and 1 steelhead) were recovered during spawning ground surveys above Rock Island.

If many of the Bonneville tags (8 of 14 or 57 percent) passed Rock Island undetected, where counters were alerted for tags of various colors and combinations, it is likely tagged fish could pass unnoticed at any dam. Unaccounted-for tags, which have been released below a dam, may not represent true mortalities of tagged fish occurring below a dam. These data are dependent upon the ability of fish counters to observe all tags, and for various reasons this may not be possible.

SUMMARY AND CONCLUSIONS

A small-scale tagging experiment below Bonneville Dam on July 14, and 15, 1955, and patterned after the Rock Island experiments, gave results similar to those obtained at Rock Island Dam. Total tag returns at Bonneville Dam were 56 percent, or somewhat less than the 64–86 percent returns at Rock Island for 1953–56. It is not known if tagged fish passed Bonneville by way of the navigation locks, thus reducing the number available for passage through the fishways. Fish released on one shore below Bonneville passed the dam through both fishways with only a slight majority passing through the Washington shore ladder on the side they were released.

The days-out period at Bonneville compared closely with the results obtained at Rock Island. The majority of tagged fish passed in 2 to 4 days at both dams. As at Rock Island Dam, the fish counters at both Bonneville and McNary Dams had difficulty in identifying species. More tagged chinooks were reported at Bonneville and McNary Dams than had been tagged.

The returns at Rock Island of the Bonneville releases were featured by the apparent inability of the counters to identify these tags. Six tags were reported at the dam and 14 were recovered on the spawning grounds above the dam. It is suggested, therefore, that tags may pass undetected at any dam and caution must be used in relating unaccounted-for tags to mortalities occurring below a dam.

OCCURRENCE IN TAMPA BAY, FLORIDA, OF IMMATURE SPECIES DOMINANT IN GULF OF MEXICO COMMERCIAL FISHERIES[1]

By James E. Sykes, *Fishery Biologist (Research Administration)*, and John H. Finucane, *Fishery Biologist (Research)*, Bureau of Commercial Fisheries

ABSTRACT

Populations of finfish, crabs, and shrimp were sampled from August 1961 through November 1962 as part of Tampa Bay estuarine studies. Specimens collected were identified to species and classified as immature or adult. Twenty-three species of major importance in Gulf of Mexico commercial fisheries were found to inhabit Tampa Bay during immaturity. Seasonal and areal distribution is described for the species common to Tampa Bay biological collections and catches in the Gulf. Although most of these species were distributed throughout the Bay system, Old Tampa Bay harbored greater numbers of them than any other area. Hillsborough Bay, an area of the system similar to Old Tampa Bay in salinity regimen, harbored fewer important species than any other area. Its relatively low production is attributed to loss of the natural habitat through human alteration. The role of the estuary in producing and rearing species important in Gulf fisheries is discussed, and the need for preservation of estuarine nursery areas is stressed.

It is becoming increasingly apparent that estuaries play an important role in the production of most finfish and shellfish harvested in coastal fisheries, and that civilization influences the nutrient capacity and productivity of these areas (Skud and Wilson, 1960).

Tampa Bay is one of the larger Gulf-connected estuaries, encompassing some 350 square miles. The primary purpose of this report is to enumerate and discuss species inhabiting this estuary in early life and entering Gulf fisheries as adults. The secondary purpose is to appraise relative species production between areas of the Bay as an aid in evaluating the probable effects on biota of the various engineering projects that are being proposed.

Man's ravages of estuarine areas in Florida are progressing so rapidly that many species of fish will disappear from these areas in the near future (Springer and Woodburn, 1960). Pollution and engineering projects are the greatest threat to the survival of estuarine species (Thompson, 1961, and Sykes, 1964 and 1965). These projects include harbor improvements, navigation channels, flood- and erosion-control structures, hurricane barriers, and fills to create new waterfront land. These alterations result in reduced water area. Adjacent bottom, including submerged grass flats, is destroyed by dredging, and the regimen of salinity and water temperature is changed. Sediments are added to the water, and damaging siltation occurs on nursery areas inhabited by commercial and sport fish species.

Although the danger to native aquatic animals is recognizable, the full significance of estuaries in the production and rearing of these organisms is not completely understood. Odum (1960) emphasized the importance of conducting research at both ends of the food chain to achieve a more complete understanding of ecological systems. He also implied that too many researchers start at a point well up on the food chain—fish, for instance—and work down. The East Gulf Estua-

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Note.—Approved for publication November 11, 1964.

[1] Contribution No. 16, Bureau of Commercial Fisheries Biological Station, St. Petersburg Beach, Fla.

rine Investigations of the Bureau of Commercial Fisheries include studies of nutrients and primary crops of estuarine waters, as well as studies of the dependence of animals such as finfish, crabs, and shrimp upon nutrients and planktonic organisms (Sykes, 1965). The research, therefore, is being conducted near both extremes of the food chain and at intermediate points. Although the value of an estuary to our social and economic system should not be measured entirely in terms of its contribution to a commercial fishery, the harvest of edible and industrial species is a major consideration and is logically one of the factors motivating estuarine research. It was, therefore, important in our investigations to determine and study the important commercial species in Gulf of Mexico fisheries that utilize estuaries as rearing and developmental areas.

TAMPA BAY, WEST FLORIDA COAST, AND GULF FISHERIES

In evaluating the importance of Tampa Bay as a nursery area for commerical species, the size and economic value of commercial catches of the Gulf of Mexico should be considered.

Fisheries in the Gulf have grown notably in the past quarter-century. In 1936, 187 million pounds or 4 percent of recorded landings were from the Gulf; in 1961, this area yielded 1.3 billion pounds or 27 percent of total recorded U.S. fishery landings (Power, 1961). Of the average annual Gulf catch for 1958, 1959, and 1960, 12 percent (131,369,000 pounds) was landed on the west coast of Florida (Power, 1960, 1961, 1962a, 1962b). Size and value of the west Florida landings were second to Texas and exceeded Louisiana, Mississippi, and Alabama.

A summary of valuation showed that the total U.S. exvessel landings in the Gulf of Mexico were worth an annual average of $85 million for the 3 years cited. West Florida landings accounted for $20 million of that amount. Catches landed in the three counties surrounding Tampa Bay (Pinellas, Hillsborough, and Manatee) averaged 26 million pounds for the 3 years and accounted for $6 million of the total (U.S. Fish and Wildlife Service, 1959; Rosen, 1959; Rosen and Robinson, 1960). Pinellas County is dominant among the three counties in landings of seafood. It has the most extensive offshore commercial and sport fishing on the Florida west coast. The county supports the second largest fleet of commercial boats, the third largest fleet of party boats, and the sixth largest fleet of charter boats in the State (Moe, 1963).

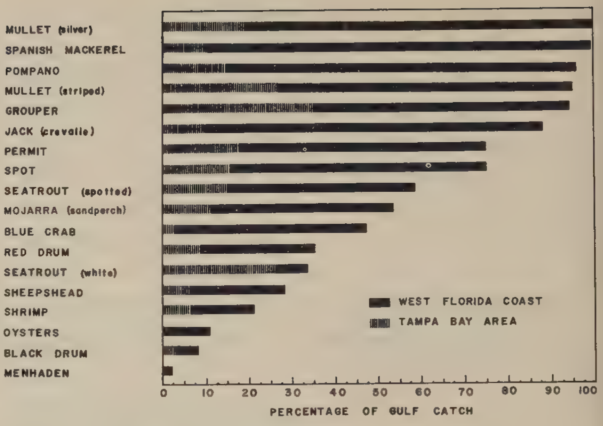

FIGURE 1.—Three year average (1958–59–60) of commercial landings on the Florida west coast and in Tampa Bay compared with total Gulf catches.

Catch data were assembled for the important commercial species common to Gulf of Mexico, Florida west coast, and Tampa Bay fisheries (table 1). For a determination of percentages of the total Gulf catch landed on the Florida coast and in Tampa Bay (fig. 1), annual landings of these species were averaged for the three divisions of Gulf fisheries for the years 1958–60.[2] Two of the leading Gulf species, menhaden and oysters, were included even though their commercial catch in the Tampa Bay area was negligible.

More than 90 percent of the Gulf landings of silver mullet, spanish mackerel, pompano, striped mullet, and grouper were made on the Florida west coast (fig. 1). Annual landings of these species for 1958–60 averaged 12 million pounds in Tampa Bay, 45 million pounds on the west coast, and 47 million pounds in the Gulf. Species comprising 25–90 percent of Gulf catches landed on the west coast were crevalle jack, permit, spot, spotted sea trout, mojarra, blue crab, red drum, white sea trout, and sheepshead. Annual landings of these species for the 3 years averaged 1.5 million pounds in Tampa Bay, 19 million pounds on the west coast, and 38 million pounds in the Gulf. Landings on the west coast of the two most important commercial species in the Gulf (shrimp and menhaden) were each below 25 percent of total

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[2] The species in table 1 and fig. 1 are listed according to percentage of Gulf catch landed on the Florida west coast rather than rank in the total Gulf catch.

TABLE 1.—*Average of 1958–60 annual landings of selected commercial species in Gulf of Mexico fisheries*

	Average Gulf landings	West Florida landings	Average 3-county[1] landings
	Pounds	*Pounds*	*Pounds*
Mullet (silver)[2]	690,300	690,300	137,900
Spanish mackerel	4,676,300	4,645,000	364,900
Pompano	506,700	486,000	66,200
Mullet (striped)	32,962,300	31,293,700	8,885,700
Grouper[2]	5,638,000	5,276,000	1,993,200
Jack (crevalle)	1,011,000	890,100	92,200
Permit	40,300	30,200	6,900
Spot	250,300	188,700	38,400
Sea trout (spotted)	4,817,700	2,821,300	652,300
Mojarra (sandperch)[2]	282,700	150,000	28,900
Blue crab	29,199,000	13,748,300	468,900
Red drum	2,009,300	712,100	152,900
Sea trout (white)	210,700	69,700	54,400
Sheepshead	378,000	107,200	23,900
Shrimp[2]	190,860,700	40,774,000	12,357,900
Oysters	13,409,000	1,380,300	1,900
Black drum	1,651,000	129,000	43,900
Menhaden[2]	678,523,000	11,092,600	4,000
Total	967,116,300	114,484,500	25,374,400

[1] Pinellas, Hillsborough, and Manatee.

[2] When several species were reported under a single common name by Federal and State statistical agents, they were listed accordingly regardless of the number of species involved.

Gulf catches. Oysters and black drum also were included in the 0–25 percent range. Average annual landings of these four species were 12 million pounds in Tampa Bay, 53 million pounds on the west coast, and 884 million pounds in the Gulf.

BIOLOGICAL COLLECTIONS

Monthly fish collections were made in the Tampa Bay area during August 1961 through November 1962. The study area encompassed the entire Tampa Bay system extending from the mouth throughout Old Tampa and Hillsborough Bays (fig. 2). The hydrological influence of the estuary extends into the Gulf for an undetermined distance; however, in this report only the semienclosed waters of Tampa Bay are regarded as estuarine habitat.

Gear used in collecting specimens consisted of 30-, 50-, and 70-foot minnow seines, a 10-foot shrimp trawl, a 16-foot balloon trawl, a 3 x 3-foot push net and a 6-foot cast net. Springer and Woodburn (1960) used similar seines, push nets, and, in addition, a roller frame trawl. In a qualitative assessment of the species occupying Tampa Bay and the sizes of these species, the collections by all types and sizes of gear were utilized and included in this report. When quantitatively describing occurrence by species and area, data were restricted to collections from the 10-foot shrimp trawl and the 50-foot seine. Duration of each trawl haul was 10 minutes at 3–4 knots. Seine operation was as similar as possible at each station throughout the study period to insure comparability of results in catch per unit of effort.

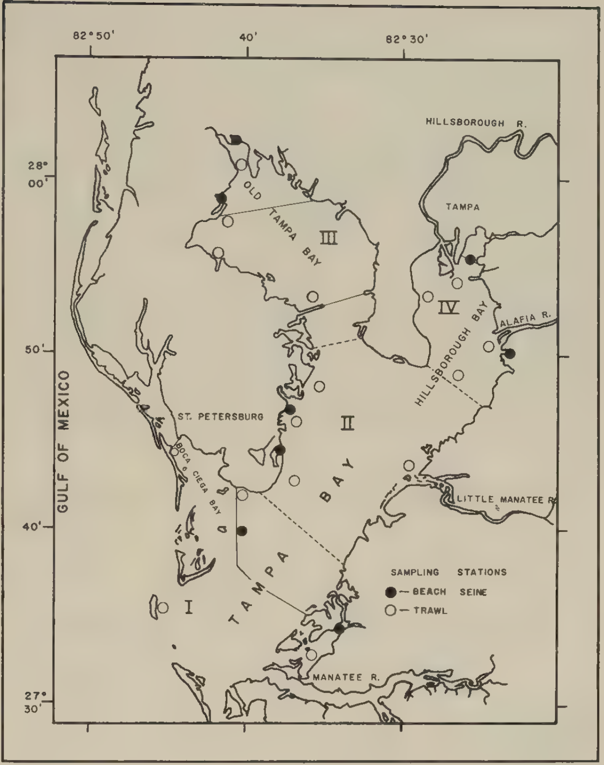

FIGURE 2.—Study areas and station locations in Tampa Bay.

Sampling stations were stratified throughout the Bay to collect specimens from the full salinity range. For comparison of species occupancy by area and salinity range, the stations were grouped to represent four areas based on salinity data from Saloman, Finucane, and Kelly (1964): Area I—lower Tampa Bay (salinity range, 21.92–37.16 °/oo, mean—31.95°/oo); Area II—central Tampa Bay (salinity range, 15.88–33.53°/oo, mean—24.48°/oo); Area III—Old Tampa Bay (salinity range, 0.09–31.83°/oo, mean—24.53°/oo); and Area IV—Hillsborough Bay (salinity range, 1.58–30.46°/oo, mean—23.63°/oo) (fig. 2).

The separation of specimens into immature or adult classes was based upon (1) observations of gonad development in relation to length frequency data compiled at the Bureau of Commercial Fisheries Biological Station at St. Petersburg, Beach, (2) published data on individual species

(Anderson, 1957; Anderson, 1958; Gunter, 1945; Guest and Gunter, 1958; Gunter and Christmas, 1960; Frisbie, 1961; Fields, 1962; Springer and Woodburn, 1960; and Rathbun, 1930), and (3) personal communication (Bonnie Eldred—Florida State Marine Laboratory, St. Petersburg, Fla. and George H. Rees—Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.).

Specimens were preserved in 10 percent formalin, and fish were measured to the nearest millimeter in standard length. The carapace of crabs (width) and shrimp (length) was measured by micrometer to the nearest one-tenth millimeter.

SUMMARIZED DATA

Fish and crustaceans from all stations and gear were classified as immature or adult to aid in assessing the utilization and dependency of each species on the estuary during early life. Although some adults were captured—and Tampa Bay sport fisheries take large numbers of them—specimens in sampling gear were limited largely to small forms. Size ranges and occurrence by section of Tampa Bay were noted (tables 2–5).

Trawl and seine catches of the commercially important finfish, shrimp, and crabs were compiled

TABLE 2.—*Size by season of commercial species of fish and crustaceans in Lower Tampa Bay—Area I, December 1961–November 1962*

Species	WINTER (Dec.–Feb.)				SPRING (Mar.–May)				SUMMER (June–Aug.)				FALL (Sept.–Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)									14	51–107			2	114–121		
Mugil trichodon (silver mullet)	94	17–157			23	34–113			58	10–90			444	16–161		
Scomberomorus maculatus (spanish mackerel)									2	35–41			1	94		
Do													6	*133–158		
Trachinotus carolinus (pompano)									2	44–56			70	42–167		
Do									64	*23–87						
Mugil cephalus (striped mullet)	817	17–32			1,234	21–86	1	230	101	50–137			41	90–154		
Mycteroperca microlepis (gag)									5	160–263			15	160–195		
Epinephelus morio (red grouper)									2	84–92						
Caranx hippos (crevalle jack)	53	120–347							4	25–52			3	37–90		
Trachinotus sp. (permit)	1	150							20	21–83			69	35–109		
Do	9	*60–74							112	*8.5–68.5			76	*24–144		
Leiostomus xanthurus (spot)	888	12–147	37	151–175	823	21–143	29	150–175	47	61–142	12	150–175	10	94–130	38	147–248
Cynoscion nebulosus (spotted seatrout)	9	43–134			1	*5.9			29	19–91	2	180–448	85	13–140	1	180
Eucinostomus gula (mojarra)	322	7–54	172	57–105	151	24–54	99	55–115	917	14–54	138	55–90	1,866	16–53	307	55–92
Eucinostomus argenteus (mojarra)	5	14–47	7	60–103	8	31–49	40	65–115	93	26–54	90	55–111	336	15–53	64	55–80
Diapterus plumieri (mojarra)	10	50–63							1	32			1	39		
Callinectes sapidus: (blue crab):																
Male	40	15.1–82.8	3	98.0–140.0	5	46.0–80.9	4	96.3–150.0	11	46.0–89.4	1	97.3	97	12.3–89.0	6	103.0–190.0
Female	38	14.8–95.6	1	168.0	10	42.8–92.1	1	138.0	11	46.4–95.2			95	11.7–96.2	2	131.0–202.2
Sciaenops ocellata (red drum)	45	18–55	1	270	2	100–124							20	19–30		
Cynoscion arenarius (white seatrout)	1	75	8	180–225	2	27–50	6	175–210	11	25–75	12	166–206	20	16–165	23	172–223
Archosargus probatocephalus (sheepshead)	3	81–170	4	185–325	2	19–21	2	180–275	14	25–44			3	51–155	10	172–285
Penaeus duorarum (pink shrimp)	290	4.8–20.0	11	20.5–26.6	16	11.1–19.9	15	20.7–28.7	664	5.2–18.0			1,070	4.3–20.0	5	20.2–24.2
Pogonias cromis (black drum)							1	*593	2	116–128			1	170		
Brevoortia patronus (menhaden)					1	75			5	70–78						
Brevoortia smithi (menhaden)					2	25–76			3	71–75					3	135–185

*From Springer and Woodburn (1960).

TABLE 3.—*Size by season of commercial species of fish and crustaceans in Central Tampa Bay—Area II, December 1961–November 1962*

Species	WINTER (Dec.–Feb.)				SPRING (Mar.–May)				SUMMER (June–Aug.)				FALL (Sept.–Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)	3	122–153	----	----	----	----	----	----	1	74	----	----	----	----	----	----
Mugil trichodon (silver mullet)	53	28–143	7	175–234	7	121–137	----	----	----	----	----	----	----	----	----	----
Scomberomorus maculatus (spanish mackerel)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Trachinotus carolinus (pompano)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Mugil cephalus (striped mullet)	187	18–24	----	----	157	24–71	----	----	16	53–87	----	----	----	----	----	----
Mycteroperca microlepis (gag)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Epinephelus morio (red grouper)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Caranx hippos (crevalle jack)	----	----	----	----	----	----	----	----	2	25–45	----	----	----	*186–246	----	----
Trachinotus sp. (permit)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Leiostomus xanthurus (spot)	256	17–30	----	----	176	24–60	----	----	21	64–130	11	165–180	13	86–125	16	152–165
Cynoscion nebulosus (spotted seatrout)	3	52–86	----	----	----	----	----	----	11	18–132	----	----	54	27–80	----	----
Eucinostomus gula (mojarra)	241	17–49	30	66–80	366	19–52	44	57–85	90	31–53	131	55–93	423	15–53	46	57–90
Eucinostomus argenteus (mojarra)	35	36–54	42	57–100	79	26–52	51	55–95	22	42–54	20	59–101	151	21–53	38	56–106
Diapterus plumieri (mojarra)	----	----	----	----	----	----	----	----	----	----	----	----	1	47	----	----
Callinectes sapidus (blue crab):																
Male	4	13.3–46.8	----		3	46.0–63.0	3	92.0–144.0	10	12.7–78.0	5	90.0–113.5	25	14.3–69.0	2	135.0–154.5
Female	7	18.5–50.9	----	----	9	40.2–110.0	----	----	3	54.2–65.7	----	----	13	15.5–68.0	4	145.0–200.0
Sciaenops ocellata (red drum)	30	21–71	----	----	1	82	----	----	----	----	----	----	18	14–37	----	----
Cynoscion arenarius (white seatrout)	----	----	----	----	----	----	----	----	15	14–125	12	165–200	1	35	12	184–227
Archosargus probatocephalus (sheepshead)	----	----	----	----	11	19–35	----	----	6	24–30	----	----	2	65–81	----	----
Penaeus duorarum (pink shrimp)	27	6.3–15.1	2	29.7–31.8	3	12.8–16.0	1	23.2	334	5.3–19.5	----	----	422	5.0–19.7	1	20.3
Pogonias cromis (black drum)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Brevoortia patronus (menhaden)	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----
Brevoortia smithi (menhaden)	----	----	----	----	2	31–36	----	----	1	*43.8	----	----	----	----	2	170–180

*From Springer and Woodburn (1960).

by month and area to compare abundance of immature animals (table 6). Catches included were from four selected trawl stations and two selected seine stations in each of the four sampling areas fished monthly. The catches of these six fishing operations in each area during 1 month represent one unit of effort. Thus, 72 hauls (12 standard units of effort) took place in each of the four areas during a 12-month period. The data allowed comparison of abundance between individual species by season and area (fig. 3). For this estimate, effort expended and numbers of specimens caught per species were combined for 3-month intervals; winter, spring, summer, and fall.

DISCUSSION

Most of the species landed by Gulf of Mexico commercial fisheries inhabit estuaries as immature, developing forms. It is assumed, therefore, that these estuaries are prime suppliers for the Gulf fisheries. Power (1962b) stated that five species—menhadan, shrimp, crabs, oysters, and mullet—comprised a catch of 1,131 million pounds or 89.3 percent of the Gulf commercial catch in 1960. Our investigations showed that 23 commercially important species including the dominant ones listed by Power (1962b) occupy Tampa Bay while immature.[3] All of these species are caught as

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[3] Oysters are included in this number but were not collected by sampling gear.

TABLE 4.—*Size by season of commercial species of fish and crustaceans in Old Tampa Bay—Area III, December 1961–November 1962*

Species	WINTER (Dec.-Feb.)				SPRING (Mar.-May)				SUMMER (June-Aug.)				FALL (Sept.-Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)	-----	-----	-----	-----	1	44	-----	-----	1	52	-----	-----	-----	-----	-----	-----
Mugil trichodon (silver mullet)	60	15–101	-----	-----	7	41–134	-----	-----	49	22–84	-----	-----	159	15–101	-----	-----
Scomberomorus maculatus (spanish mackerel)	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1	*36	-----	-----
Trachinotus carolinus (pompano)	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Mugil cephalus (striped mullet)	1,011	17–32	4	155–165	3,434	21–130	-----	-----	511	42–122	-----	-----	3	92–126	1	210
Mycteroperca microlepis (gag)	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Epinephelus morio (red grouper)	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Caranx hippos (crevalle jack)	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Trachinotus sp. (permit)	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Leiostomus xanthurus (spot)	1,279	12–135	17	151–157	3,170	21–139	15	149–190	486	40–137	20	155–189	262	66–133	61	150–185
Cynoscion nebulosus (spotted seatrout)	1	36–105	1	210	1	29	1	180	158	14–147	5	165–225	37	33–147	1	410
Eucinostomus gula (mojarra)	8	30–52	37	62–90	-----	-----	11	55–84	9	32–50	8	65–73	25	26–48	17	55–80
Eucinostomus argenteus (mojarra)	175	13–50	29	59–85	30	34–50	18	56–86	48	21–46	11	57–74	253	12–50	52	56–83
Diapterus plumieri (mojarra)	153	55–75	-----	-----	-----	-----	-----	-----	728	15–65	7	87–103	123	27–74	-----	-----
Callinectes sapidus (blue crab):																
Male	40	12.3–88.0	8	93.6–195.0	47	40.0–88.7	16	90.5–180.0	19	39.0–87.0	59	92.0–140.0	30	18.0–83.5	38	90.5–163.0
Female	21	16.0–108.0	1	150.0	52	20.0–127.0	2	135.0–145.0	16	12.5–115.8	11	130.0–155.0	36	16.0–125.0	2	150.0–152.0
Sciaenops ocellata (red drum)	55	24–89	-----	-----	2	102–114	-----	-----	-----	-----	-----	-----	147	14–62	-----	-----
Cynoscion arenarius (white seatrout)	6	55–140	2	192–198	6	35–49	3	210–258	307	17–95	6	155–195	164	20–118	4	160–215
Archosargus probatocephalus (sheepshead)	1	125	-----	-----	7	16–30	-----	-----	3	40–63	-----	-----	4	66–132	1	171
Penaeus duorarum (pink shrimp)	31	5.7–19.5	12	20.5–30.1	4	13.3–19.8	9	21.1–30.1	124	6.5–18.8	7	20.7–28.9	478	3.5–19.8	9	20.5–25.8
Pogonias cromis (black drum)	-----	-----	-----	-----	-----	-----	-----	-----	5	37–156	-----	-----	1	197	-----	-----
Do	-----	-----	-----	-----	1,064	*20–75	-----	-----	57	*66–110	-----	-----	-----	-----	-----	-----
Brevoortia patronus (menhaden)	1	*22.1	-----	-----	135	24–74	-----	-----	33	58–115	-----	-----	1	105	-----	-----
Do	-----	-----	-----	-----	-----	-----	-----	-----	8	*55–108	-----	-----	-----	-----	-----	-----
Brevoortia smithi (menhaden)	-----	-----	-----	-----	263	21–46	-----	-----	19	59–91	-----	-----	-----	-----	-----	-----
Do	-----	-----	-----	-----	-----	*19–29.1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

*From Springer and Woodburn (1960).

adults in Gulf of Mexico commercial fisheries and Tampa Bay sport fisheries. Few constitute important commercial fisheries in Tampa Bay. The significance of the estuary lies more in the growth of species for later harvest in Gulf fisheries than in catches of adults in nursery areas.

Shrimp comprise the most valuable fishery in the Gulf of Mexico (Power, 1962b). Commercial catches consist primarily of three species: the brown shrimp, *Penaeus aztecus;* the white shrimp, *P. setiferus;* and the pink shrimp, *P. duorarum* (Kutkuhn, 1962). Young of several species in developmental stages have been found in Tampa Bay (Eldred, Ingle, Woodburn, Hutton, and Jones, 1961)—the penaeid shrimp, *Trachypeneus constrictus* and *P. duorarum,* and the rock shrimp, *Sicyonia laevigata* and *S. typica.* These and one additional penaeid species, *Trachypeneus similis,* were identified in our collections (Saloman, 1964).

The important Gulf shrimp collected in Tampa Bay was *P. duorarum.* It is estimated that 75 percent of the shrimp brought to dock in the three-county area surrounding Tampa Bay are *P. duorarum* and 25 percent *P. setiferus.* Ninety-eight percent of the total is actually caught on the Campeche grounds (personal communication, Robert Benton—Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas). In Tampa Bay, *P. duorarum* is caught for a bait-shrimp market only. During October 1961

TABLE 5.—*Size by season of commercial species of fish and crustaceans in Hillsborough Bay—Area IV, December 1961–November 1962*

Species	WINTER (Dec.-Feb.)				SPRING (Mar.-May)				SUMMER (June-Aug.)				FALL (Sept.-Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Mugil trichodon (silver mullet)	3	29–35	-----	----------	4	71–96	-----	----------	-----	----------	-----	----------	19	15–25	-----	----------
Scomberomorus maculatus (spanish mackerel)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	1	240
Trachinotus carolinus (pompano)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Mugil cephalus (striped mullet	10	19–100	-----	----------	83	22–88	-----	----------	63	56–115	-----	----------	4	121–153	-----	----------
Mycteroperca microlepis (gag)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Epinephelus morio (red grouper)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Caranx hippos (crevalle jack)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Trachinotus sp. (permit)	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Leiostomus xanthurus (spot)	12	18–30	-----	----------	367	27–137	18	158–176	25	70–135	3	155–175	3	95–110	12	145–165
Cynoscion nebulosus (spotted seatrout)	5	91–109	-----	----------	-----	----------	-----	----------	5	42–88	-----	----------	1	86	-----	----------
Eucinostomus gula (mojarra)	2	19–53	3	75–85	1	42	-----	----------	-----	----------	-----	----------	1	43	-----	----------
Eucinostomus argenteus (mojarra)	70	25–50	7	58–85	9	35–51	10	63–91	73	24–50	1	65	156	16–51	17	60–68
Diapterus plumieri (mojarra)	81	33–77	4	131–145	-----	----------	-----	----------	2	30–45	-----	----------	14	47–74	-----	----------
Callinectes sapidus (blue crab):																
Male	7	40.4–79.6	1	166.0	30	11.0–80.2	19	92.0–153.0	3	53.2–87.2	5	97.1–149.0	13	11.8–87.3	23	93.0–163.0
Female	6	28.0–87.2	2	132.0–175.0	19	42.0–120.0	-----	----------	-----	----------	-----	----------	7	20.5–115.0	1	164.0
Sciaenops ocellata (red drum)	131	27–72	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------	3	21–55	-----	----------
Cynoscion arenarius (white seatrout)	11	114–153	4	170–221	14	18–45	10	170–210	29	17–83	1	181	36	17–142	36	166–248
Archosargus probatocephalus (sheepshead)	17	111–170	-----	----------	1	24	-----	----------	5	30–133	-----	----------	13	93–167	-----	----------
Penaeus duorarum (pink shrimp)	18	10.5–18.4	12	29.1–33.5	-----	----------	-----	----------	3	9.9–17.4	-----	----------	47	5.9–19.4	10	20.6–27.3
Pogonias cromis (black drum)	-----	----------	-----	----------	-----	----------	-----	----------	16	48–114	1	278	1	165	-----	----------
Brevoortia patronus (menhaden)	-----	----------	-----	----------	1	55	-----	----------	-----	----------	-----	----------	-----	----------	-----	----------
Brevoortia smithi (menhaden)	-----	----------	-----	----------	7	23–28	1	241	179	33–69	-----	----------	2	87–93	2	159–172

TABLE 6.—*Numbers of immature specimens of fish and crustaceans taken in sampling gear by month, December 1961–November 1962, Tampa Bay, Fla.*

	Numbers of fish, shrimp, crabs				Total per month
	Area I	Area II	Area III	Area IV	
1961					
Dec	54	22	103	35	214
1962					
Jan	102	76	539	14	731
Feb	315	414	627	36	1,392
Mar	182	261	1,975	164	2,582
Apr	22	277	2,016	254	2,569
May	13	259	725	96	1,093
Jun	33	107	1,028	260	1,428
July	252	157	641	44	1,094
Aug	674	122	493	88	1,377
Sept	346	215	76	100	737
Oct	325	531	249	36	1,141
Nov	227	258	116	88	689
Total per area	2.545	2,699	8,588	1,215	15,047
Catch/unit effort	212.1	225.0	715.7	101.2	----------

through April 1962, 71,000 pounds of bait shrimp were caught in this fishery (Saloman, 1965).

Eldred et al. (1961) described recruitment of postlarval *P. duorarum* into Tampa Bay and a movement of larger shrimp from the Bay to offshore waters. Their observations on migration and our collections of larvae suggest that at least part of the Gulf shrimp fishery for that species depends upon populations developed in Tampa Bay.

Menhaden ranks first in size of catch and next to shrimp in value for all species landed in the Gulf of Mexico. The fishery in the Gulf depends upon catches of *Brevoortia patronus* (Gunter and Christmas, 1960). *B. smithi* and *B. gunteri* have been found in the Gulf, and probably comprise a very small fraction of the commercial catch.

There is no menhaden fishery in Tampa Bay, and landings of menhaden on the Florida west coast are minor in relation to total Gulf landings.

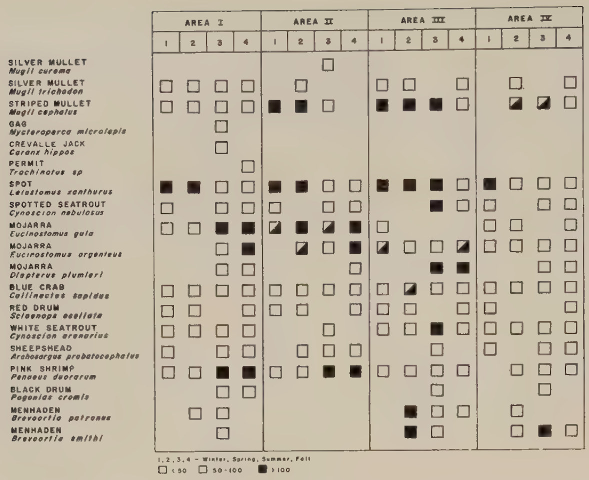

FIGURE 3.—Occurrence of immature commercial species of fish and crustaceans by season and area, Tampa Bay, Fla., December 1961–November 1962.

Gunter and Christmas (1960) and Reintjes (1961) observed that menhaden spawn at sea and subsequently move as larvae into estuaries which serve as nursery areas for further development. Collections in Tampa Bay by our staff and by Springer and Woodburn (1960) showed that Tampa Bay is a rearing area for two species of menhaden: *B. patronus* and *B. smithi*. *B. smithi* was more abundant and more widely distributed in our samples than *B. patronus;* the reverse of their occurrence in Gulf catches. Suttkus (1958) stated that *B. smithi* occurs in the eastern Gulf and that *B. patronus* overlaps *B. smithi* in the northeastern Gulf at Cedar Keys, Fla. Tabb and Manning (1960) reported only one species, *B. smithi*, from Florida Bay in the southern portion of the State. These findings suggest that normally *B. smithi* would be more abundant than *B. patronus* in central Florida or the Tampa Bay area.

Mullet ranked third in pounds landed in the Gulf and second both in Tampa Bay and on the Florida west coast. Heavy dependence upon the estuary was exhibited in that three species, *Mugil cephalus*, *M. trichodon*, and *M. curema*, were found in immature and adult stages. The striped mullet, *M. cephalus*, is dominant in Bay catches (Rosen and Ellis, 1958).

The blue crab, *Callinectes sapidus*, besides being prominent in Gulf fisheries, is harvested commercially in Tampa Bay. Also, it is the object of a large sport fishery. The species forms the most rapidly expanding fishery in Florida (Rosen and Robinson, 1960). Approximately 50 percent of the reported Tampa Bay landings (table 1) were actually caught in the Bay, and the remaining 50 percent were caught in Citrus County to the north of Tampa Bay and adjacent to the Gulf of Mexico.

C. sapidus was the dominant portunid in collections of metamorphosed and identifiable specimens. Numerous portunid zoeae and megalops also were taken. We were unable to make positive species identification at these stages and therefore cannot estimate the proportion of *C. sapidus* in the collections. Sandoz and Rogers (1944) stated that a salinity range of 23–30°/₀₀ is ideal for hatching blue crabs. Thus, from a salinity standpoint, the Bay appears to offer a favorable environment for hatching and development of blue crabs. This fact and the presence of adult blue crabs as well as portunid larvae led us to believe that the blue crab is reared within the confines of Tampa Bay. In addition to mature adults, the young identifiable metamorphosed forms (50-mm. carapace width) which inhabit the Bay are most abundant in winter.

The American oyster (*Crassostrea virginica*) is an estuarine resident and supports relatively small but growing commercial and sport fisheries in Tampa Bay. The actual harvest in the Bay is probably many times larger than the reported harvest (table 1). A portion of the beds is public, and fleets of small, privately owned boats tong for oysters there. In recent years, interest has been generated toward the possibility of increasing the numbers and sizes of the beds in Tampa Bay. Decreased oyster production in Chesapeake Bay has brought some oystermen into Florida from that area.

Of the 19 species of fish and crustaceans (fig. 3), 13 were taken in all four sections of Tampa Bay. This indicates that all of the Bay is used as a nursery area. Eighteen species were taken in the lower, high salinity portion of the Bay (Area I), 13 in the central portion (Area II), 15 in Old Tampa Bay where lowered salinities prevail (Area III), and 15 in Hillsborough Bay (Area IV), also an area of reduced salinity. The commercially important species of fish, shrimp, and crabs are euryhaline and, as expected, were distributed throughout the Bay system. The differences among numbers of species inhabiting sections of the Bay appeared to be of little or no consequence. This appraisal, however, is exclusive of those species not considered to be of commercial importance in this report.

Catch per unit of effort data made it possible to determine whether immature animals had a preference of habitat among areas of the Tampa Bay system (table 6). An overwhelming preference was apparent for Old Tampa Bay (Area III) where there were three times as many total animals as in either Lower or Central Tampa Bay (Areas I and II) and seven times as many as in Hillsborough Bay (Area IV). Abundance in Area III exceeded that of Areas I, II, and IV during 9 months out of 12. Although peak abundance varied between areas and time periods, March and April produced the greatest number of specimens per unit of effort from the collective areas.

Data on abundance of individual species by area and season also indicate an areal preference (fig. 3). Seven species were taken in numbers greater than 100 during at least one season (three units of effort) in Area III, five in Area II, four in Area I, and two in Area IV. The data indicate, therefore, that Area III (Old Tampa Bay) produces or develops more individuals during a greater portion of the year than any other area of the Tampa Bay system, and that Hillsborough Bay is the least productive of commercially important species.

Based on the known salinity preference of many euryhaline animals, it was expected that the greatest abundance of important species would be found in the low salinities of Old Tampa and Hillsborough Bays. Pearson (1929) and Gunter (1945, 1950) showed that a cycle of spawning, growth, and movement bore a distinct relation to salinity for many valuable fishes and invertebrates on the Gulf of Mexico coast. Salinity lower than that which is characteristic of the ocean is one of the requisites in early development of these animals. Abundance in Hillsborough Bay, however, was not nearly as great as in Old Tampa Bay. Because annual salinity patterns of Hillsborough Bay and Old Tampa Bay are similar, the difference in abundance of valuable species between the two areas must result from other environmental factors.

The introduction of industrial and domestic sewage is common in Hillsborough Bay. Natural flushing has not kept pace with the deposition of the effluents and has resulted in the accumulation of silt-size sediments throughout the Bay. Noxious compounds in solution, unstable and uninhabitable sediments, and insufficient dissolved oxygen appear to have contributed to a decline in Hillsborough Bay fisheries within a relatively short period of time.

As a nursery area for fish and crustaceans, Hillsborough Bay is no longer productive. Commensurate with alterations in bottom type and water quality, littoral areas which once supported a luxuriant growth of marine grasses are now barren except for the seasonal appearance of some red and blue-green algae.

In contrast, Old Tampa Bay remains in a relatively undisturbed state supporting blue crab, bait shrimp, and oyster fisheries, and serving as a nursery area for estuarine dependent fauna. Although industrial and residential interests continually threaten this area, it is vegetated with turtle grass (*Thalassia testudinum*), shoal grass (*Diplanthera wrightii*), cord or manatee grass (*Syringodium filiforme*), the red mangrove (*Rhizophora mangle*), and the black mangrove (*Avicennia nitida*) (Springer and Woodburn, 1960). The emergent vegetation aids in controlling the introduction of particulate detritus in surface water run-off before it enters the Bay.

Biologically, the water quality is good, and the predominantly firm sediment pattern creates a substrate suitable for the habitation of dense aggregations of benthic invertebrates. The stability of the bottom also promotes water clarity necessary for the existence of dense stands of marine algae and sea grasses which extend around the entire periphery of the area. The algae-sea grass ecosystem appears to be absolutely essential for survival and growth of juvenile stages of many commercially important species.

We conclude that the relatively undisturbed conditions of Old Tampa Bay and the fact that its salinity distribution is ideally suited to the development of many euryhaline fishes are responsible for its comparatively good productivity.

Many species recorded as inhabiting the estuary were omitted from our lists in this report. Some of these contribute indirectly but significantly to commercial fisheries by serving as food for marketable species. An example of an outstanding forage species is the scaled sardine (*Harengula pensa-*

colae). It is produced in and inhabits the Tampa Bay area in great abundance throughout most of the year. The sardine is utilized heavily as a live bait in Tampa Bay and the adjacent Gulf areas. Other forage species abundant in the estuary are the tidewater silverside (*Menidia beryllina*), the bay anchovy (*Anchoa mitchilli*), the pinfish (*Lagodon rhomboides*), the thread herring (*Opisthonema oglinum*), and the silver perch (*Bairdiella chrysura*).

The number of species of finfish, shrimp, and crabs recorded from the Tampa Bay area now stands at 265 (Springer and Woodburn, 1960; Dragovich and Kelly, 1964). Most of these probably occupy an important ecological niche in the estuary and supply food to commercial and sport species of both Gulf and Bay. Obviously, a portion of the harvest of major fisheries in the Gulf is connected directly to the production and development of young forms in Tampa Bay. This is especially true of species found in catches of the eastern Gulf or on the Florida west coast. This estuary, of course, is not the only one important in the role of supplying Gulf fisheries. Sykes (1965) estimated that some 7,500 square miles or 4.8 million acres of estuarine area exist on the periphery of the Gulf.

The general public tends to view Tampa Bay either as an area of good but declining sport fishing or as an area for waterfront homesites. The present and future importance of Tampa Bay as a food source should be taken into account when proposals are filed for permission to enclose areas with bulkheads or create land masses in the estuary. This is especially true when such structures will divert currents, allow encroachment of high-salinity waters into upper areas, or otherwise significantly alter rearing areas of the species discussed.

SUMMARY

Biological collections showed that the five most important species in Gulf of Mexico commercial fisheries inhabit Tampa Bay in immature stages of development. Eighteen species of less importance in Gulf catches were also found in immature stages in the Bay. The qualitative distribution of species exhibited little difference between salinity range and area of the Bay system but numerically Old Tampa Bay, an area of relatively low salinity contained the greatest number of animals. The importance of Tampa Bay as a nursery area for species of fish, crustaceans, and mollusks comprising the most valuable portions of the commercial fisheries in the Gulf has not been stressed in the past. This role now must be recognized because of acceleration of engineering projects in the estuary that impair its value as a nursery ground.

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GILL NET MESH SELECTION CURVES FOR PACIFIC SALMON ON THE HIGH SEAS

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ABSTRACT

Gill net mesh selection curves of normal distribution were developed and applied to Pacific salmon caught by research vessels on the high seas of the North Pacific Ocean and the Bering Sea. Mesh selection curves were constructed for pink, sockeye, and chum salmon for each of four mesh sizes, 2½-, 3¼-, 4½-, and 5¼-inch. Catch efficiency curves for combined mesh sizes show that the range for salmon lengths was covered, although the coverage was not equal for all lengths. The length-frequency distribution of each species was adjusted for effect of gill net selectivity. Adjustments were minor.

The Bureau of Commercial Fisheries fishes experimentally for salmon with surface gill nets on the high seas of the North Pacific Ocean and the Bering Sea. Salmon samples taken by gill nets are used to estimate abundance, distribution, racial identity, and growth of salmon populations in the ocean. Accurate estimates of abundance, distribution, racial identity, and growth require unbiased samples from salmon populations in the ocean. Gill nets are selective; a particular mesh size of gill net selects a particular size range of fish. To cover the range of fish sizes, four gill net mesh sizes, 2½-, 3¼-, 4½-, and 5¼-inch, stretched measure, of multifilament nylon twine are used in the fishing. Selectivity studies are necessary to assess the adequacy of this coverage and to adjust the salmon size frequencies for any bias caused by selectivity. Determining the shape and extent of the mesh selection curve for each mesh size and for combined mesh sizes is necessary before size frequencies can be adjusted for possible bias.

A METHOD FOR DETERMINING GILL NET SELECTIVITY

Holt (1957) described a method for determining gill net mesh selection curves with normal frequency distributions. He developed normal mesh selection curves for Fraser River sockeye salmon (from Peterson, 1954) and for North Sea herring (from Hodgson, 1933). He used the ratio of catches from adjacent pairs of mesh sizes at different length classes to develop parameters for the normal curve. The following formulations were abstracted from Holt (1957) and McCombie and Fry (1960):

$$C_L = nP_L p_m \cdot e^{-(L-L_m)^2/2S^2} \quad (1)$$

where C_L is the number of fish of length L caught, n the number of operations or the fishing duration, P_L the number of fish of length L liable to capture, p_m the fishing power of the mesh at the mean selection length, e the base of natural logarithms, L_m the mean selection length caught, and S the standard deviation of distribution. The ratio of catches for two meshes (A and B), differing slightly in size and fishing together, can be de-

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scribed by an equation of the linear form, $y = bL + a$:

$$\log \frac{{}_BC_L}{{}_AC_L} = \frac{({}_BL_m - {}_AL_m) \cdot L}{S^2} + \frac{{}_AL^2{}_m - {}_BL^2{}_m}{2S^2} + \log \frac{B^P{}_m}{A^P{}_m} \quad (2)$$

in which ${}_BC_L$ is the catch of length L taken in mesh B, ${}_BL_m$ is the mean selection length of mesh B, $B^P{}_m$ is the fishing power of mesh B, etc. The log $\frac{B^P{}_m}{A^P{}_m}$ term will cancel; i.e., log 1=0, by assuming that the two nets have equal fishing power for their respective mean lengths. If the terms from equation (2) are used, $\log \frac{{}_BC_L}{{}_AC_L} = y$, $\frac{{}_BL_m - {}_AL_m}{S^2} = b$ (the slope), and $\frac{{}_AL^2{}_m - {}_BL^2{}_m}{2S^2} = a$ (the y intercept). When equation (2) holds true, a plot of $\log \frac{{}_BC_L}{{}_AC_L}$ against various values of L gives a straight line, and the assumption is justified that the mesh selection curve is normal.

The selection curve parameters, ${}_AL_m$, ${}_BL_m$, and S, are obtained as follows:

$$a/b = \frac{{}_AL_m{}^2 - {}_BL^2{}_m}{2S^2} \bigg/ \frac{{}_BL_m - {}_AL_m}{S^2}$$

$$-2a/b = {}_BL_m + {}_AL_m$$

Assume that L_m is proportional to mesh size (θ). Assign a proportionality constant (K). Then, ${}_AL_m + {}_BL_m = -2a/b = K({}_A\theta A_B\theta)$, from which ${}_AL_m$ and ${}_BL_m$ can be derived. S can be found from either a or b. With these values and a table of ordinates for normal distribution (Snedecor, 1956), mesh selection curves can be constructed.

APPLICATION OF METHOD TO SALMON GILL NET CATCHES

I have applied the above analytical procedure to length frequencies of three salmon species: pink, sockeye, and chum. To illustrate the method, I have used catch data for 1957 and 1959. In these years the three species were well represented in the gill net catches of the research vessels. Catch data on sockeye and chum salmon for 1956, 1958, and 1960 were used in part of the analysis. Table 1 shows the number of the three species caught and measured during 1956 to 1960. The catches were made during May to September on the high seas of the North Pacific Ocean (north of lat. 45° N.) and the Bering Sea.

PINK SALMON

Table 2 gives the length-frequency distributions of pink salmon taken by the 3¼-, 4½-, and 5¼-inch mesh gill nets in 1957. Table 3 gives similar data for 1959. Catches were confined to three mesh sizes; the 2½-inch mesh did not catch pink salmon. Since more of the 4½-inch mesh than of the 3¼- and 5¼-inch meshes was used in a fishing set, catches of the 4½-inch mesh were reduced to equalize fishing effort. A 1:3 reduction was necessary in 1957; a 1:6 reduction in 1959. Length frequencies were grouped by 3-cm. length classes. Fork length is related to mesh size.[1]

Tables 2 and 3 also give catch ratios of adjacent mesh sizes, 4½/3¼-inch and 5¼/4½-inch. The catch ratio at each length class is limited to a combined sample size of 50 or more fish for the paired mesh sizes. By establishing a minimum sample size of 50, I was able to omit smaller samples that may not have been representative

TABLE 1.—*Gill net catches of pink, sockeye, and chum salmon by U.S. research vessels in the North Pacific Ocean and the Bering Sea, 1956–60*

Species ¹	Number of salmon caught and measured				
	1956	1957	1958	1959	1960
Pink	431	3, 129	174	4, 202	1, 049
Sockeye	3, 224	3, 584	1, 177	6, 462	8, 296
Chum	3, 565	4, 678	3, 744	6, 082	5, 816

¹ Coho and chinook salmon are excluded because of small catches.

TABLE 2.—*Catch by mesh size and catch ratio of adjacent mesh sizes, pink salmon, 1957*

Fork length (midpoint of length class)	Catch by mesh size ¹				Catch ratio	
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 4½/ 3¼-inch	log 5¼/ 4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*		
35	----------	2	----------	----------	----------	----------
38	----------	14	1	----------	----------	----------
41	----------	148	69	1	−0. 76	−4. 27
44	----------	192	363	13	+. 64	−3. 32
47	----------	42	300	32	+2. 00	−2. 24
50	----------	3	109	47	+3. 51	−. 84
53	----------	1	19	22	----------	----------
56	----------	----------	8	5	----------	----------
59	----------	1	1	1	----------	----------

¹ Original catches of the 4½-inch mesh were 3 times as large as shown; they were divided by 3 to equalize fishing effort between mesh sizes.

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[1] Mesh size as shown is factory-labeled size. During the 1960 fishing operations about 400 meshes from the four mesh sizes were measured. The average measured size was either identical to the factory-labeled size or slightly oversize.

Table 3.—*Catch by mesh size and catch ratio of adjacent mesh sizes, pink salmon, 1959*

Fork length (midpoint of length class)	Catch by mesh size [1]				Catch ratio	
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 4½ 3¼-inch	log 5¼ 4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*		
32		1				
35		3				
38		7				
41		38	26		−0.39	
44		16	201	6	+2.53	−3.51
47		6	236	14	+3.67	−2.83
50		1	135	51	+4.90	−0.97
53		1	46	49		+0.07
56		1	14	30		
59			3	3		
62		1		3		

[1] Original catches of the 4½-inch mesh were 6 times as large as shown; they were divided by 6 to equalize fishing effort between mesh sizes.

The natural logarithm of the catch ratio is directly related to the length of pink salmon for 1957 and 1959 (fig. 1). The straight lines are fitted by the least squares method. The relation in both years is approximately linear. Holt showed in equation (2) that this relation must be linear if the mesh selection curve is normal. With replicating evidence for 2 years, I feel justified in assuming that the mesh selection curve for pink salmon is approximately normal.

To obtain the normal frequency curve for each mesh size, the mean selection length and the standard deviation of the curve were needed. The estimation of these parameters for 1959 pink salmon is shown in table 4 and the determination of the normal curve in table 5.

A further step in applying the method was to construct a composite selection curve from the mesh selection curves of the three mesh sizes (fig. 2). This composite curve was obtained by summing at each length class the ordinate heights of the individual curves (table 6), as was done by McCombie and Fry (1960). The composite curve can be called a "catch efficiency curve" because

Table 4.—*Estimation of mean selection length and standard deviation of mesh selection curves, pink salmon, 1959*

Mesh sizes	Sum of mesh sizes	Sum of mean selection lengths (−2a/b)	Mean selection length	Standard deviation of selection curve
	Centimeters	*Centimeters*	*Centimeters*	*Centimeters*
3¼-inch (8.26 cm.)			34.8	
3¼ and 4½-inch	19.69	81.36		4.9
4½-inch (11.43 cm.)			48.1	
4½ and 5¼-inch	24.77	105.65		4.4
5¼-inch (13.34 cm.)			56.2	
Mean	22.23	93.50		

$K=93.50/22.23=4.21$.

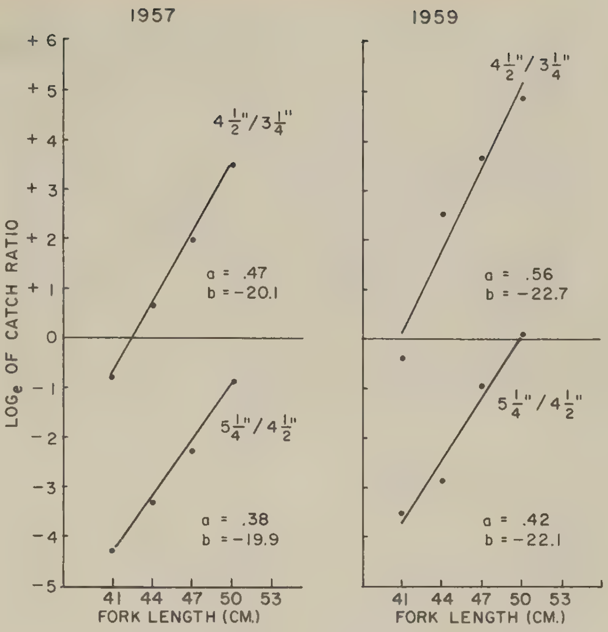

Figure 1.—Catch ratio of adjacent mesh sizes by fork length, pink salmon, 1957 and 1959.

Table 5.—*Determination of ordinate heights of normal curve for each mesh size, pink salmon, 1959*

Fork length (midpoint of length class)	3¼-inch mesh $L_m=34.8$, $S=4.9$ [1]		4½-inch mesh $L_m=48.1$, $S=4.6$ [2]		5¼-inch mesh $L_m=56.2$, $S=4.4$	
	$\frac{L-L_m}{S}$	Ordinate height	$\frac{L-L_m}{S}$	Ordinate height	$\frac{L-L_m}{S}$	Ordinate height
Centimeters						
32	0.57	0.339	3.50	0.001		
35	.04	.399	2.85	.007		
38	.65	.323	2.20	.036	4.23	0
41	1.27	.178	1.54	.122	3.55	.001
44	1.88	.068	.89	.268	2.77	.009
47	2.49	.018	.24	.388	2.09	.045
50	3.10	.003	.41	.367	1.41	.148
53	3.71	0	1.07	.225	.73	.306
56			1.72	.091	.05	.398
59			2.37	.024	.64	.325
62			3.02	.004	1.32	.167

[1] L_m=mean selection length (cm.), S=standard deviation (cm.).
[2] Mean of 4.9 and 4.4.

Table 6.—*Summation of ordinate heights of three mesh selection curves, pink salmon, 1959*

Fork length (midpoint of length class)	Ordinate height (by mesh size)			Sum of ordinate heights
	3¼-inch	4½-inch	5¼-inch	
Centimeters				
32	0.339	0.001		0.340
35	.399	.007		.406
38	.323	.036	0	.359
41	.178	.122	.001	.301
44	.068	.268	.009	.345
47	.018	.388	.045	.451
50	.003	.367	.148	.518
53	0	.225	.306	.531
56		.091	.398	.489
59		.024	.325	.349
62		.004	.167	.171

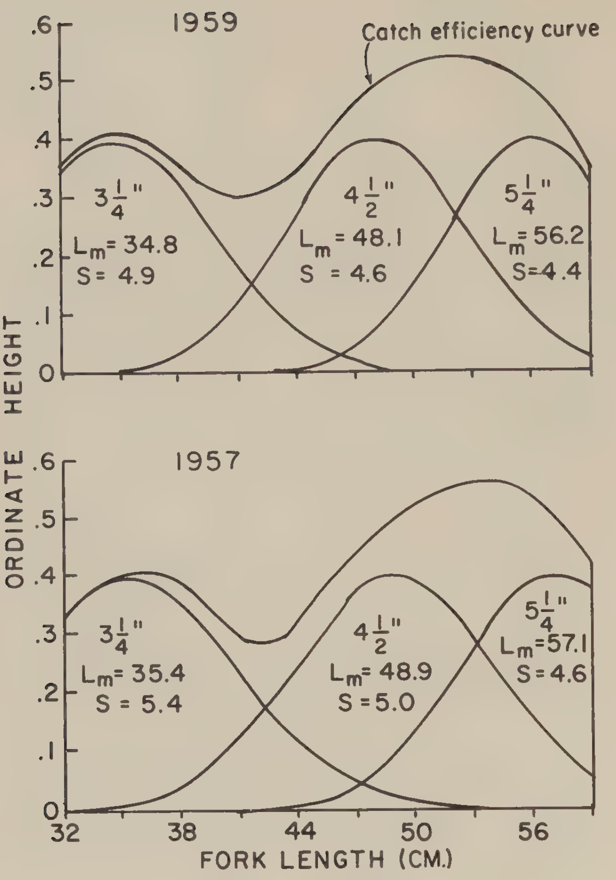

Figure 2.—Catch efficiency curve (sum of ordinate heights at each length) for three mesh sizes combined, pink salmon, 1957 and 1959.

it shows a relative catch efficiency of gill nets over fish length range. Curves for 1957 and 1959 are shown.

In both years the catch efficiency curves show a dip at 41 cm. Catch efficiency at 41 cm. is lower because of the 1¼-inch gap between the 3¼- and 4½-inch mesh sizes. The gap between the 4½- and 5¼-inch meshes is ¾ inch.

The final step in applying the method was to reconstruct the length frequency curve of the available fish population, adjusting for effect of gill net selectivity. The uncorrected catch was divided by the sum of ordinates at each length class (table 7). The corrected catch for all length classes was the length frequency curve adjusted for effect of gill net selectivity.

When the uncorrected and the corrected length frequency distributions of pink salmon taken by combined mesh sizes of gill net in 1957 and 1959

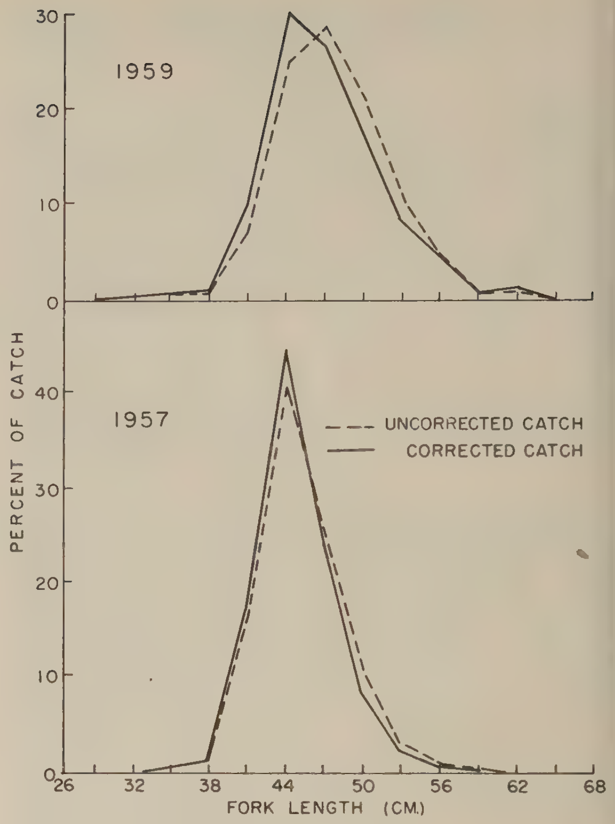

Figure 3.—Length frequency distribution of pink salmon adjusted for effect of gill net selectivity, 1957 and 1959.

are plotted, a single mode of maturing 2-year-old fish is evident (fig. 3).

Adjustments for gill net selectivity in 1957 were minor. In the uncorrected catches the 41-cm. and 44-cm. length classes were slightly under-represented and the 47-cm., 50-cm., and 53-cm. classes were slightly over-represented. The corrected catch curve adjusts for these conditions. The mode, after I adjusted for selectivity, remains unchanged at 44 cm.

In 1959 the amount of correction was somewhat greater than in 1957. As in 1957, the 41-cm. and 44-cm. lengths were under-represented, the 47-cm., 50-cm., and 53-cm. lengths over-represented. Adjustments in 1959 changed the position of the mode from 47 cm. to 44 cm.

SOCKEYE SALMON

Least squares lines were fitted to the catch ratios of sockeye salmon taken in 1959 by the four gill net mesh sizes (fig. 4). Catch data are in table 8. Catch ratios were computed for

TABLE 7.—*Adjustment of 1959 catches of pink salmon for effect of gill net selectivity*

Fork length (midpoint of length class)	Uncorrected	Sum of ordinate heights	Corrected	Uncorrected	Corrected
Centimeter	*Number*		*Number*	*Percent*	*Percent*
32	1	0. 340	3	0. 1	0. 1
35	3	. 406	7	. 3	. 3
38	7	. 359	19	. 8	. 9
41	64	. 301	213	7. 2	10. 0
44	223	. 345	646	25. 0	30. 3
47	256	. 451	568	28. 7	26. 7
50	187	. 518	361	21. 0	16. 9
53	96	. 531	181	10. 8	8. 5
56	45	. 489	92	5. 0	4. 3
59	6	. 349	17	. 7	. 8
62	4	. 171	23	. 5	1. 1

samples of 50 or more fish, as was done for pink salmon. Sockeye salmon catch ratios for each pair of mesh sizes showed approximate linearity over the greater part of the range of fish lengths, but not at the extremes of the range. Approximate linearity extended from 29 cm. to 38 cm. for the 3¼/2½-inch mesh sizes, from 38 cm. to 53 cm. for the 4½/3¼-inch mesh sizes, and from 47 cm. to 62 cm. for the 5¼/4½-inch mesh sizes. Least squares lines were fitted in these ranges. The procedure of discarding extremes in line-fitting previously was used by Garrod (1961).

Figure 5 shows a similar picture for 1957 (data are in table 9). Catch ratios were approximately linear except at the extremes. In 1957 and 1959 similar length ranges were used in line-fitting, except for extending the range to 41 cm. for the 3¼/2½-inch mesh sizes in 1957.

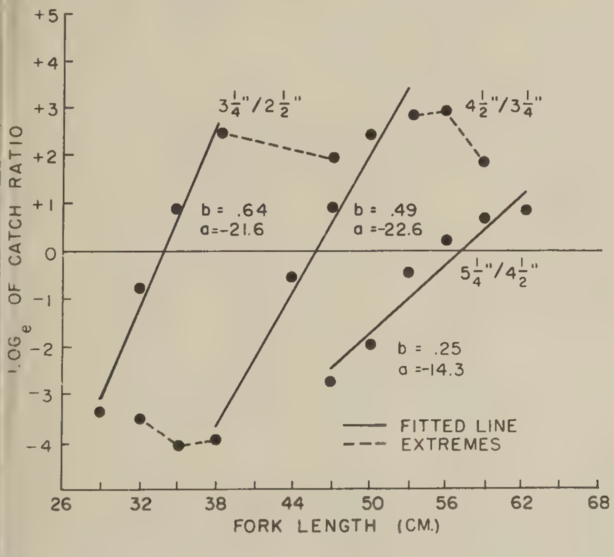

FIGURE 4.—Catch ratio of adjacent mesh sizes by fork length, sockeye salmon, 1959.

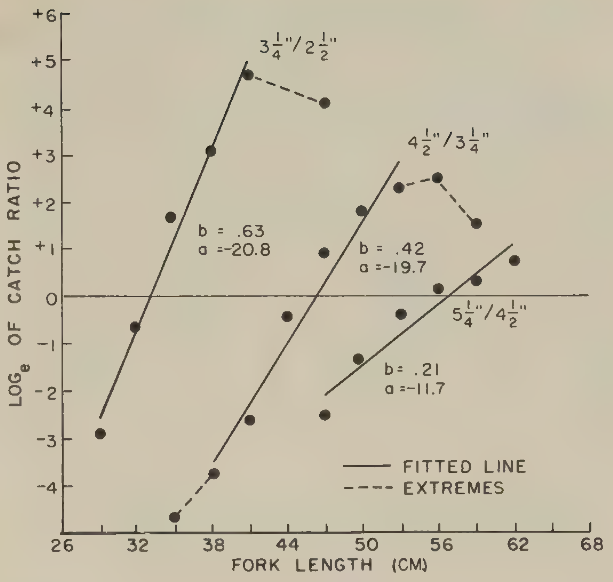

FIGURE 5.—Catch ratio of adjacent mesh sizes by fork length, sockeye salmon, 1957.

TABLE 8.—*Catch by mesh size and catch ratio of adjacent mesh sizes, sockeye salmon, 1959*

Fork length (midpoint of length class)	Catch of sockeye by mesh size [1]				Catch ratio		
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 3¼/ 2½-inch	log 4½/ 3¼-inch	log 5¼/ 4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
26	9	--------	--------	--------	--------	--------	--------
29	88	3	--------	--------	−3. 38	--------	--------
32	293	139	4	4	−. 75	(−3. 54)	--------
35	279	648	9	7	+. 85	(−4. 27)	--------
38	22	268	5	2	+2. 50	−3. 96	--------
41	1	34	2	--------	--------	−2. 85	--------
44	1	41	23	2	--------	−. 58	--------
47	6	44	111	7	(+1. 99)	+. 92	−2. 76
50	1	16	161	23	--------	+2. 40	−1. 94
53	3	9	155	97	--------	+2. 84	−. 47
56	--------	9	118	144	--------	(+2. 94)	+. 19
59	3	9	59	116	--------	(+1. 88)	+. 68
62	--------	6	22	51	--------	--------	+. 82
65	2	4	4	22	--------	--------	--------
68	1	--------	1	5	--------	--------	--------
74	--------	--------	--------	1	--------	--------	--------

[1] Original catches of the 4½-inch mesh were 6 times as large as shown; they were divided by 6 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

Catch ratios showing the linear relation represent mainly fish which were enmeshed (gilled) around the head and gill cover by the net twine. Catch ratios departing from the straight line at either end were discarded because they represent large fish snagged or small fish tangled in the gill nets.

In the 1959 sockeye catch ratios of the 4½/3¼-inch mesh sizes (fig. 4), the discarded catch ratios at 32 cm. and 35 cm. and at 56 cm. and 59 cm. curve away from the fitted line, giving the effect of a tipped S-shaped curve. At 32 cm. and 35 cm. the fish in the 4½-inch mesh were probably

Table 9.—*Catch by mesh size and catch ratio of adjacent mesh sizes, sockeye salmon, 1957*

Fork length (midpoint of length class)	Catch of sockeye by mesh size [1]				Catch ratio		
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 3¼/ 2½-inch	log 4½/ 3¼-inch	log 5¼/ 4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
23	4						
26	36	1					
29	55	3			−2.90		
32	54	29	1	1	−.62		
35	32	168	2	1	+1.66	(−4.62)	
38	8	176	4	1	+3.09	−3.77	
41	1	108	8		+4.68	−2.60	
44		46	31	3		−.40	
47	1	57	133	11	(+4.04)	+.85	−2.49
50	3	34	194	50		+1.74	−1.36
53	4	15	146	100		+2.28	−.38
56	3	9	108	121		(+2.48)	+.11
59	3	20	84	114		(+1.44)	+.31
62	2	11	26	54			+.73
65		4	6	20			
68	1	1	1	1			
71				1			

[1] Original catches of the 4½-inch mesh were 3 times as large as shown; they were divided by 3 to equalize fishing effort between mesh sizes.

Note.—Catch ratios in parentheses were not used. See text.

tangled rather than gilled. At 56 cm. and 59 cm. the fish in the 3¼-inch mesh were mainly snagged rather than gilled. Some fish within the 38-cm. to 53-cm. length range also were snagged or tangled, but the numbers were so small that the linear relation between fish length and log of catch ratio was unaffected.

The procedure for developing mesh selection curves and a catch efficiency curve for sockeye salmon followed that for pink salmon. Table 10 shows the summation of the ordinate heights of the mesh selection curves for the four mesh sizes. The composite curve was used to adjust for selectivity effect (table 11).

A comparison of the uncorrected and corrected length frequency distributions of sockeye salmon in 1957 and 1959 shows that the 44-cm. and 47-cm. fish are under-represented, the 53-cm. to 59-cm. over-represented in the uncorrected catches (fig. 6). Over most of the length range, adjustments were quite minor.

Adjustments for the effect of gill net selectivity changed slightly the shape of the length-frequency distribution curve of sockeye salmon. The length-frequency distributions in 1957 and 1959 were bimodal. Mode 1 consisted of small fish (highly abundant in 1959) that had spent one winter at sea. Mode 2 consisted of large fish that

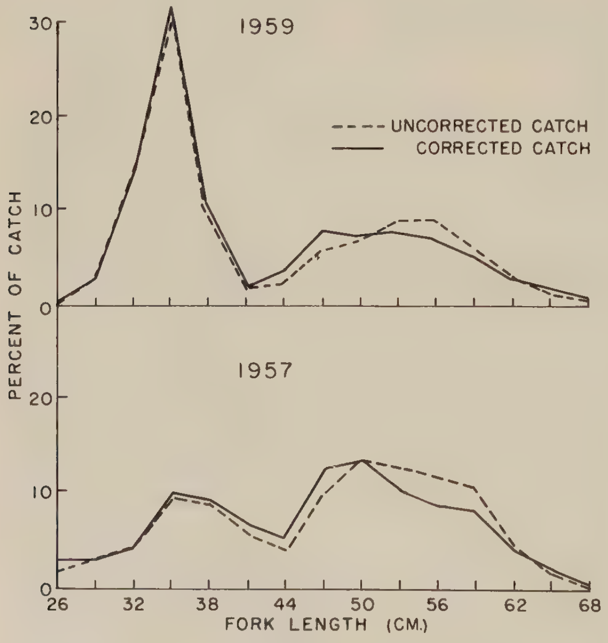

Figure 6.—Length frequency distributions of sockeye salmon adjusted for effect of gill net selectivity, 1957 and 1959.

Table 10.—*Summation of ordinate heights of four mesh selection curves, sockeye salmon, 1959*

Fork length (midpoint of length class)	Ordinate height (by mesh size)				Sum of ordinate heights
	2½-inch	3¼-inch	4½-inch	5¼-inch	
Cm.					
26	0.268	0.013			0.281
29	.398	.056			.454
32	.306	.165	0		.471
35	.122	.319	.003		.444
38	.025	.391	.014	0	.430
41	.003	.327	.049	.001	.380
44	0	.176	.124	.005	.305
47		.062	.242	.019	.323
50		.014	.357	.060	.431
53		.002	.398	.142	.542
56		0	.337	.259	.596
59			.216	.365	.581
62			.106	.398	.504
65			.039	.335	.374
68			.011	.218	.229

Table 11.—*Adjustment of the 1959 catches of sockeye salmon for effect of gill net selectivity*

Fork length (midpoint of length class)	Un-corrected	Sum of ordinate heights	Corrected	Un-corrected	Corrected
Centimeter	*Number*		*Number*	*Percent*	*Percent*
26	9	0.281	32	0.3	0.5
29	91	.454	201	2.9	2.9
32	440	.471	944	14.2	13.8
35	943	.444	2,158	30.5	31.4
38	297	.430	678	9.6	9.9
41	37	.380	97	1.2	1.4
44	67	.305	218	2.2	3.2
47	168	.323	525	5.4	7.6
50	201	.431	472	6.5	6.9
53	264	.542	491	8.5	7.2
56	271	.596	455	8.8	6.6
59	187	.581	321	6.0	4.7
62	79	.504	156	2.6	2.3
65	32	.374	85	1.0	1.2
68	7	.229	30	.2	.4
74	1	(.044)			

Note.—Length class 74 cm. was omitted.

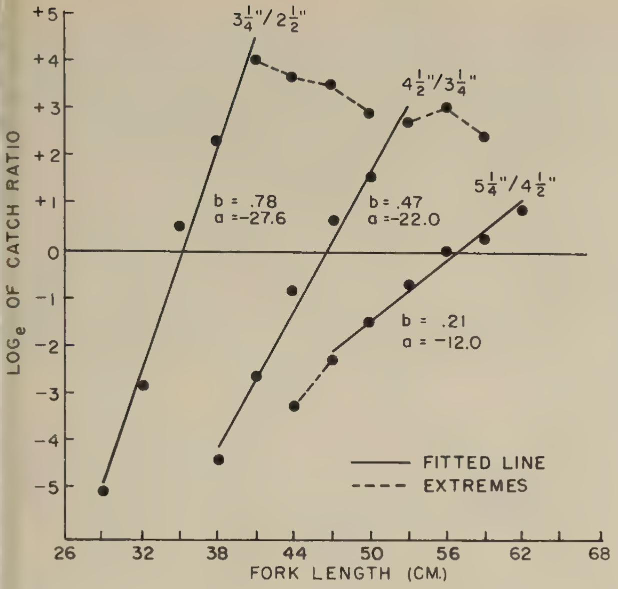

FIGURE 7.—Catch ratio of adjacent mesh sizes by fork length, chum salmon, 1957.

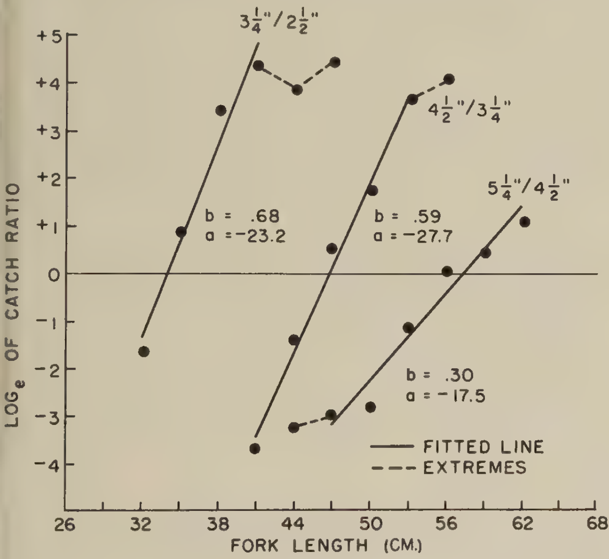

FIGURE 8.—Catch ratios of adjacent mesh sizes by fork length, chum salmon, 1959.

had spent mainly two and three winters at sea. Mode 1 did not change position, but mode 2 shifted to smaller fish when adjusted for selectivity. This change occurred in both years.

Chum salmon

The problems encountered for chum salmon and the results obtained are almost identical to those for sockeye salmon. As with sockeye, chum salmon catch ratios of a minimum 50-fish sample for each pair of mesh sizes were approximately linear over a greater part of the range of fish lengths but not at the extremes. The length ranges for chum salmon were identical to those established for sockeye. Least squares lines were fitted to the 1957 and 1959 catch ratios of the three pairs of mesh sizes (figs. 7 and 8). Catches on which these lines were based are given in tables 12 and 13. Table 14 sums up the ordinate heights for the four mesh sizes.

TABLE 12.—*Catch by mesh size and catch ratio of adjacent mesh sizes, chum salmon, 1957*

Fork length (mid-point of length class)	Catch of chum by mesh size [1]				Catch ratio		
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 3¼/2½-inch	log 4½/3¼-inch	log 5¼/4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
26	5	--------	--------	--------	--------	--------	--------
29	330	2	1	1	−5.12	--------	--------
32	523	28	--------	2	−2.92	--------	--------
35	52	89	--------	1	+.54	--------	--------
38	8	78	1	--------	+2.28	--------	--------
41	2	109	8	--------	+4.00	--------	--------
44	3	119	52	2	(+3.68)	−0.83	(−3.27)
47	3	100	191	21	(+3.50)	+.65	−2.21
50	3	58	285	64	(+2.96)	+1.59	−1.49
53	1	13	203	105	--------	+2.75	−.66
56	--------	6	117	105	--------	(+2.97)	−.01
59	1	4	46	66	--------	(+2.44)	+.36
62	--------	--------	16	41	--------	--------	+.94
65	--------	--------	5	15	--------	--------	--------
68	--------	--------	2	10	--------	--------	--------
71	--------	--------	--------	1	--------	--------	--------
74	--------	--------	--------	1	--------	--------	--------

[1] Original catches of the 4½-inch mesh were 3 times as large as shown; they were divided by 3 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

TABLE 13.—*Catch by mesh size and catch ratio of adjacent mesh size, chum salmon, 1959*

Fork length (mid-point of length class)	Catch of chum by mesh size [1]				Catch ratio		
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 3¼/2½-inch	log 4½/3¼-inch	log 5¼/4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
29	9	--------	--------	--------	--------	--------	--------
32	57	11	--------	1	−1.64	--------	--------
35	18	44	1	--------	+ .89	--------	--------
38	3	93	--------	1	+3.42	--------	--------
41	2	156	4	--------	+4.36	--------	--------
44	4	196	48	2	(+3.89)	−3.65	(−3.22)
47	1	84	160	8	(+4.43)	−1.41	−3.00
50	1	37	232	14	--------	+.53	−2.81
53	2	5	195	67	--------	+1.78	−1.08
56	--------	2	113	116	--------	+3.66	+.03
59	--------	--------	59	95	--------	(+4.03)	+.50
62	--------	2	14	45	--------	--------	+1.17
65	--------	--------	4	24	--------	--------	--------
68	--------	--------	--------	4	--------	--------	--------
71	--------	--------	--------	2	--------	--------	--------

[1] Original catches of the 4½-inch mesh were 6 times as large as shown; they were divided by 6 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

Figure 9 and table 15 show the uncorrected and corrected length-frequency distributions of chum

TABLE 14.—*Summation of ordinate heights of four mesh selection curves, chum salmon, 1959*

Fork length (midpoint of length class)	Ordinate height (by mesh size)				Sum of ordinate heights
	2½-inch	3¼-inch	4½-inch	5¼-inch	
Cm.					
26	0.242	0.006			0.248
29	.393	.033			.426
32	.319	.122	0		.441
35	.130	.280	.001		.411
38	.026	.395	.005		.426
41	.003	.341	.024	0	.368
44	0	.180	.078	.001	.259
47		.060	.187	.007	.254
50		.012	.323	.030	.365
53		.001	.398	.091	.490
56		0	.352	.201	.553
59			.223	.331	.554
62			.102	.398	.500
65			.033	.352	.385
68			.008	.228	.236

salmon. In 1957 and 1959 the corrected catches increased at 44 cm. and 47 cm. and decreased at 53 cm. to 59 cm. As with sockeye, the mode of the large chum salmon shifted to smaller fish when adjusted for selectivity.

SELECTIVITY COMPARED FOR THE THREE SPECIES

The catch efficiency of the combined mesh sizes was compared for pink, sockeye, and chum salmon (fig. 10). Curves were given for sockeye and chum salmon ranging in length from 29 cm. to 62 cm. and for pink salmon from 38 cm. to 56 cm.; these covered 98 percent of the samples. Chum and sockeye curves are similar and show a dip in catch efficiency at 44 cm. and 47 cm., resulting from the 1¼-inch gap between the 3¼- and 4½-inch mesh sizes. Both curves show peak catch efficiency at 56 cm. and 59 cm. The mode for sockeye is about 56 cm., for chum about 57 cm. The pink salmon curve shows peak catch efficiency at 53 cm. and lowest catch efficiency at 41 cm.

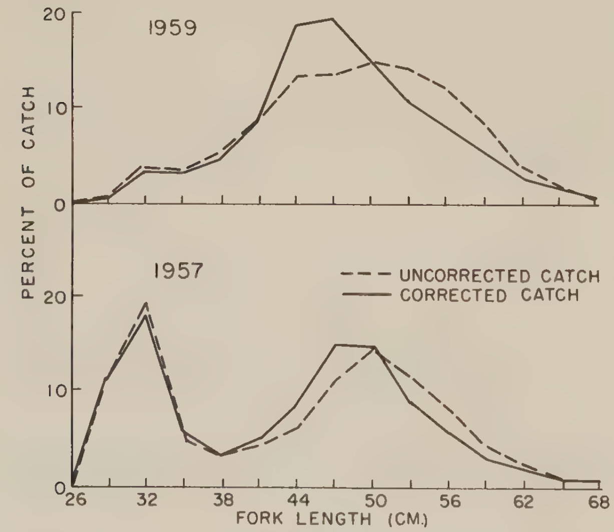

FIGURE 9.—Length frequency distribution of chum salmon adjusted for effect of gill net selectivity, 1957 and 1959.

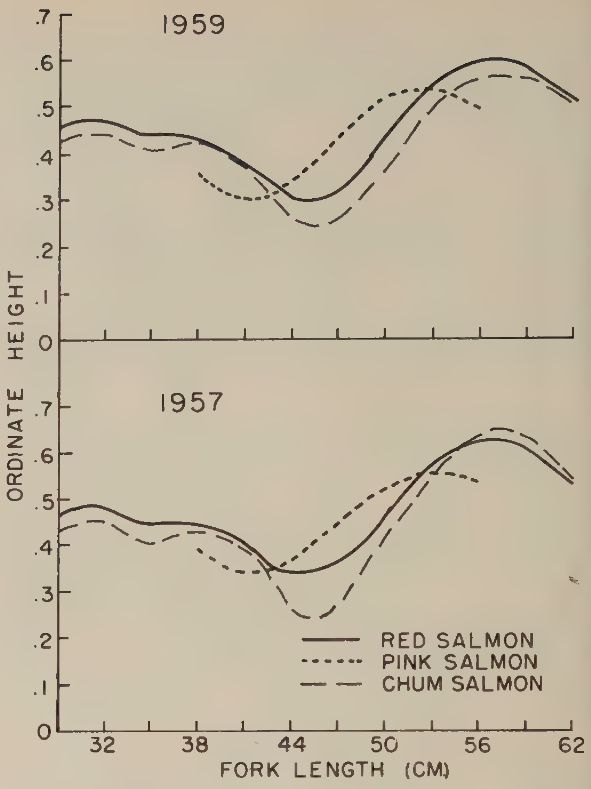

FIGURE 10.—Comparison of catch efficiency of combined mesh sizes on pink, sockeye, and chum salmon, 1957 and 1959.

TABLE 15.—*Adjustment of the 1959 catches of chum salmon for effect of gill net selectivity*

Fork length (midpoint of length class)	Uncorrected	Sum of ordinate heights	Corrected	Uncorrected	Corrected
Centimeters	*Number*		*Number*	*Percent*	*Percent*
29	9	0.426	21	0.5	0.4
32	69	.441	156	3.6	3.0
35	63	.411	153	3.3	2.9
38	97	.426	228	5.0	4.4
41	162	.368	440	8.4	8.5
44	250	.259	965	12.9	18.6
47	253	.254	996	13.1	19.2
50	284	.365	778	14.7	15.0
53	269	.490	549	13.9	10.6
56	231	.553	418	11.9	8.0
59	154	.554	278	8.0	5.4
62	61	.500	122	3.2	2.3
65	28	.385	73	1.4	1.4
68	4	.236	17	.2	.3
71	(2)	(.176)			

NOTE.—Length class 71 cm. was omitted.

The shape of the catch efficiency curves for sockeye and chum salmon between 44 cm. and 62 cm. and for pink salmon between 38 cm. and 56 cm. is somewhat similar. The pink salmon curve is displaced to shorter fish. Pink salmon probably have greater girth per given length than the other two species, although no girth measurements of pink salmon were taken to verify this. Differences shown in figure 10 probably result from girth/length differences among the three species.

DISCUSSION

Certain assumptions in applying Holt's method were considered. One assumption was that standard deviations of selection curves should be similar. A computation of the S values for each year from 1956 to 1960 checked this assumption. Table 16 lists S values for each pair of mesh sizes. Sockeye and chum salmon S values are given for all years. Pink salmon S values were computed only for odd-numbered years; catches were small in even-numbered years.

Standard deviations of selection curves within each species were reasonably similar in at least the larger mesh sizes, 3¼-, 4½-, and 5¼-inch. Pink salmon had slightly higher S values and sockeye slightly lower S values in the paired 3¼- and 4½-inch mesh sizes than in the 4½- and 5¼-inch (table 16). Chum salmon also varied only slightly between these sizes. In the 2½- and 3¼-inch pair of mesh sizes, however, the S values for sockeye and chum salmon were low. The small 2½-inch mesh was probably the main cause of these low values.

Table 16.—*Standard deviation of mesh selection curves for pink, sockeye, and chum salmon by year*

Salmon species	Year	Standard deviation (paired mesh sizes)		
		2½-inch and 3¼-inch	3¼-inch and 4½-inch	4½-inch and 5¼-inch
		Centimeters	*Centimeters*	*Centimeters*
Pink	1957	-----------	5.4	4.6
Do	1959	-----------	4.9	4.4
Sockeye	1956	3.5	5.5	6.1
Do	1957	3.7	5.9	6.5
Do	1958	3.1	5.1	6.1
Do	1959	3.9	5.5	5.9
Do	1960	4.0	5.4	6.3
Chum	1956	3.6	5.6	5.3
Do	1957	3.4	5.6	6.5
Do	1958	3.7	4.4	5.5
Do	1959	3.6	5.0	5.4
Do	1960	3.8	5.2	5.1

Another assumption was that the mean selection length of salmon is proportional to mesh size. Mesh size (perimeter) is directly related to the fish's girth. Lander (1963) showed that the girth and length of sockeye and chum salmon of the high seas have a linear relation. Thus, the relation of length of salmon and mesh size warrants using proportionality constants (K values).

K values within species varied remarkably little annually (table 17). Between species, K values for pink salmon were lower than those for sockeye and chum salmon, probably because pink salmon have greater girth per given length. As shown in table 17, mean selection lengths had lower values in pink salmon than in the other two species.

All investigators did not use normal distribution for the mesh selection curve. Some used a skewed mesh selection curve, tailing off to the right, rather than a normal curve. Olsen (1959), working with Newfoundland herring data, found that logs of catch ratios followed a parabolic line better than a straight line. His selection curves, thus, are slightly skewed rather than normal. Ishida (1962) used a mesh-size ratio method in developing skewed selectivity curves for salmon from the North Pacific. Gulland and Harding (1961), using gill net catches of the African catfish *Clarias*, obtained a skewed selection curve with a long upper tail. The shape of *Clarias* (long fish with a large bony head) and the method of its capture (entanglement in

Table 17.—*Proportionality constants and mean selection lengths for pink, sockeye, and chum salmon*

Salmon species	Year	K[1]	Mean selection length by mesh size			
			2½-inch 6.35 cm.	3¼-inch 8.26 cm.	4½-inch 11.43 cm.	5¼-inch 13.34 cm.
			cm.	*cm.*	*cm.*	*cm.*
Pink	1957	4.28	27.2	35.4	48.9	57.1
Do	1959	4.21	26.7	34.8	48.1	56.2
		Mean	27.0	35.1	48.5	56.6
Sockeye	1956	4.53	28.8	37.4	51.8	60.4
Do	1957	4.62	29.3	38.2	52.8	61.6
Do	1958	4.49	28.5	37.1	51.3	59.9
Do	1959	4.62	29.3	38.2	52.8	61.6
Do	1960	4.60	29.2	38.0	52.6	61.4
		Mean	29.0	37.8	52.3	61.0
Chum	1956	4.63	29.4	38.2	52.9	61.8
Do	1957	4.68	29.7	38.7	53.5	62.4
Do	1958	4.68	29.7	38.7	53.5	62.4
Do	1959	4.67	29.7	38.6	53.4	62.3
Do	1960	4.73	30.0	39.1	54.1	63.1
		Mean	29.7	38.7	53.5	62.4

[1] K=Proportionality constant of fish length divided by mesh size.

several meshes) are thought to cause the asymmetry.

Other investigators besides Holt used normal distribution for mesh selection curves. McCombie and Fry (1960), working with Lake Huron whitefish data, concluded that normal distribution best describes the mesh selection curve. Using nylon gill net catches of *Tilapia* from Lake Victoria, East Africa, Garrod (1961) showed that normal distribution applies over most of the selection range of fish lengths but not at the extremes of this range. Garrod used the normal curve obtained from linear regression after discarding the extremes where the relation departs from linear. I also used the procedure of discarding the extremes and then applying the normal curve.

SUMMARY

1. A method for determining gill net selectivity described by Holt (1957) was applied to experimental gill net catches of pink, sockeye, and chum salmon from the high seas of the North Pacific Ocean and Bering Sea. This method develops mesh selection curves for gill nets of different mesh sizes from catch ratios at various fish lengths.

2. A normal mesh selection curve, representing relative catch efficiency of the mesh for different length classes of fish, was constructed for each mesh size, 2½-, 3¼-, 4½- and 5¼-inch, for each species. Normal distribution can be used validly when extreme sizes of fish caught by snagging and tangling rather than gilling are omitted.

3. A composite curve of relative catch efficiencies for combined mesh sizes shows that the four mesh sizes cover the range of salmon lengths. All length classes were not caught with equal efficiency. A lower catch efficiency at 44 cm. of 47 cm. for sockeye and chum salmon and 41 cm. for pink salmon, resulted from the larger (1¼-inch) gap between the 3¼- and 4½-inch mesh sizes. The gap between other adjacent mesh sizes was three-quarter inch.

4. The composite curve for each species was used to adjust gill net catches for selectivity effect. Adjustments were minor.

ACKNOWLEDGMENTS

R. H. Lander helped with the mesh selection theory, F. C. Cleaver made suggestions for writing the report, and W. F. Royce reviewed the report.

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LIFE HISTORY OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM* (LE SUEUR), IN WESTERN LAKE ERIE

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ABSTRACT

The rapid increase in the stocks of gizzard shad in Lake Erie since 1950 unquestionably had an important effect on the ecology of the lake. The present study, based on almost 24,000 fish collected by various means in 1952–55 in or near the island area of western Lake Erie was undertaken to provide information on the role of shad in the bionomics of the region.

The annulus of the gizzard shad scale is a valid yearmark. It is laid down in May–July, a little later in the older than in the younger fish. The body-scale relation is linear with an intercept of 22.1 mm. on the axis of standard length. Age-groups 0, I, and II were abundantly represented in the samples. Age-group III was was much less well represented, and older fish were extremely scarce. The oldest shad seen belonged to the VI-group.

The seasonal growth was most rapid in July–August and growth was much reduced or nil in January–April. Males attained the following average standard lengths (in millimeters) at the end of the indicated years of life: 1–141; 2–273; 3–313; 4–343; 5–349. For females these values were: 1–140; 2–285; 3–335; 4–364; 5–386.

The weight of the gizzard shad increased as the 3.07053 power of the length. The length-weight relation varied seasonally, annually, and, near the spawning season, according to sex and state of gonads.

Although the gizzard shad is distributed widely throughout the Mississippi Valley and in stream systems tributary to the Gulf of Mexico and the Atlantic Coast north to about lat. 40° N., some question exists as to whether it is native to the Great Lakes-St. Lawrence basin or has penetrated into this region in historic times. Gerking (1945) was of the opinion that this fish migrated from the Mississippi drainage into the glacial Great Lakes during the Lake Maumee outlet stage. Kirtland (1850) believed that it gained access to Lake Erie from the Mississippi drainage recently by way of various Ohio canal connections. Trautman (1957), on the other hand, thinks that the gizzard shad was present in Lake Erie waters before the advent of the canals. Miller (1957) believed the question of whether the shad is native to Lake Erie cannot be solved conclusively.

The establishment of gizzard shad in Lake Erie in large numbers appears to have taken place fairly recently, however, and their presence in Lakes Huron, Michigan, and Ontario became known subsequent to collections of the species along the south shore of Lake Erie. The report of gizzard shad in the St. Lawrence River at Quebec is of recent date. Fresh-water fishery investigations—especially of rough fish—were so meager prior to 1850 that shad could easily have been overlooked.

In the Great Lakes-St. Lawrence drainage the gizzard shad has been reported from Lake Michigan in the west to Quebec in the east, but it has become best established along the western and southern shores of Lake Erie and in streams tributary to these shores.

The role of the gizzard shad in the ecology of fish populations is difficult to assess. Its value as a link in the food chain is not to be questioned. On the other hand, no use for shad other than as forage fish has been developed and their rapid growth soon makes them too large for most predatory fish. Shad tend to overpopulate many waters to a degree that seems to be detrimental to other species. In some southern states reduction of numbers of shad is part of the fish-management program for certain waters.

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In the past years, the numbers of gizzard shad in Lake Erie were too few for the species to create any important problems, indeed, to have any real significance in the bionomics of the lake, but recently their abundance has increased enormously. Mass mortalities have created esthetic and public-health problems, water intakes have been plugged, and commercial fishermen have wasted hours sorting and discarding the worthless shad from their catches. From the fish-management standpoint, the question arises whether the value of shad as forage may not now be outweighed by their diversion of the productive capacity of the lake into commercially valueless fish. An inquiry into the natural history of the gizzard shad in Lake Erie, accordingly, has been much needed.

Only a few precocious male and female gizzard shad attain sexual maturity as age group I. Almost all males and a good percentage of females mature at age II and only rarely are III-group shad immature. Development of the egg and seasonal changes of the ovary are described. Egg production is highest in the II group—average of 378,990 per individual and 689 per gram of body weight. Spawning takes place from early June into July and is most intensive near mid-June. Heaviest spawning is at water temperatures of 67° F. or more. Early development to the attainment of the adult shape is described; particular attention is given to the development of the alimentary tract.

The anatomy of the digestive tract in the adult is described and comments are offered on the function of such organs as the pharyngeal pouches and the caeca. Tests were made for digestive enzymes in different parts of the tract. The gizzard shad is a filter feeder. Food varies widely with season and locality but consists mostly of phytoplankton and zooplankton.

The gizzard shad population has been increasing in Lake Erie. Commercial fishermen told me that 3 decades ago the "sawbelly" was something of a rarity—only an occasional one was caught. They have attained greatest abundance, according to these fishermen, since about 1950. Whether this increase results from adaptations to the Lake Erie environment, to changes in the character of the lake, or merely to increasing surpluses of shad beyond environmental and predatory inroads has not been determined.

Gizzard shad seem to be most plentiful in the shallow waters around the periphery of western Lake Erie, in the Bass Islands area, and especially in protected bays and mouths of tributaries. The numbers present here vary from season to season. They are most numerous in late summer and early fall when their abundance is increased by the recruitment of the young of the year. They are next most plentiful just prior to and during their spawning season in late spring when the mature shad congregate in the shallow waters. Then, too, in winter they concentrate in places into which warm streams flow. At other times they are rarely seen in numbers—frequently days go by without any captures of shad by the commercial fishermen of South Bass Island.

The tendency of shad to inhabit shallow water, their attraction in massive numbers to the warmer water of outlets from industrial plants and of inflowing streams, and the frequent mass mortalities doubtless have given rise to an exaggerated idea of their abundance. Nevertheless, they are plentiful and their numbers are growing. The shad problem is real in both a practical and a purely scientific sense.

MATERIALS AND METHODS

The investigation of the life history of the gizzard shad was based on almost 24,000 fish (about two-thirds of which were young of the year) captured in western Lake Erie and in streams tributary to the southwestern shore of this lake in 1952–55. Studies of age, length, weight, growth, reproduction, and fecundity were made for shad captured in the lake. Fish caught in Sandusky Bay and in the tributary streams were omitted from those phases of the study because of differences in growth and other aspects of their life history.

The Sandusky Bay specimens were decidedly smaller than lake fish of the same age and appeared to have formed their annuli earlier in the year. Also, they probably spawned earlier than the lake-dwelling gizzard shad. The water in Sandusky Bay was frequently turbid—the shallow water is readily turned over by winds. Phytoplankton, though reduced by this turbidity, is not lacking, for much is washed into the bay from the marshes by the tributary streams. Stomach contents of fish caught in Sandusky Bay were largely muddy. The slower growth of the fish here probably

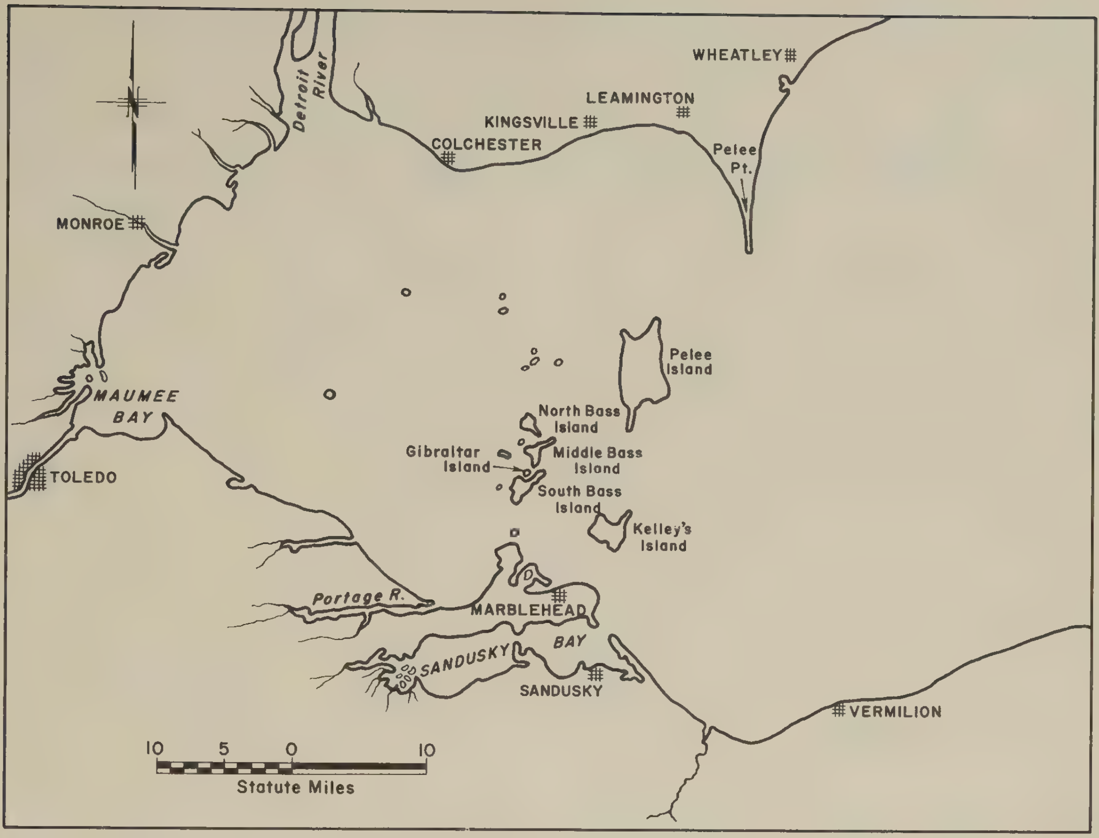
Detroit River
WHEATLEY
LEAMINGTON
KINGSVILLE
COLCHESTER
Pelee Pt.
MONROE
Pelee Island
MAUMEE BAY
North Bass Island
Gibraltar Island
Middle Bass Island
TOLEDO
South Bass Island
Kelley's Island
Portage R.
MARBLEHEAD
BAY
SANDUSKY
SANDUSKY
VERMILION
10
5
0
10
Statute Miles

FIGURE 1.—Western Lake Erie where gizzard shad were collected in 1952–55.

resulted from the reduced nutriment. The earlier annulus formation and spawning are undoubtedly related to the earlier warming of the shallow waters in the bay.

The gizzard shad caught in the streams were not as deep-bodied as either the lake or the Sandusky Bay fish; and they were smaller, age for age, than those captured in Sandusky Bay. They were thinner, more gracefully shaped individuals, seemingly better adapted for swimming in streams. Probably the colder water and the poorer food supply were responsible for their slower growth.

Methods, Dates, and Sites of Collection

With the exception of gizzard shad from Sandusky Bay or tributary streams and a few otter trawl collections in the open lake, all samples were captured in western Lake Erie within one-half of a mile of island or mainland shores (fig. 1).

Gizzard shad were captured in the deeper water by 5-inch mesh (stretched measure) gill nets and standard commercial trap nets. Closer to shore, in 4 to 10 feet of water, I collected them by means of 4-inch mesh gill nets, experimental gill nets with meshes ranging from 1 to 4 inches, dynamite, rotenone, and electric shocks. In waters less than 4 feet deep, along the shore, I used "Common Sense" seines, a push seine, bag seine, and dip net. In Sandusky Bay the fishermen employed haul seines. See table 1 for methods of collection for each month and year and table 2 for methods of collection for each locality.

Data Recorded for Individual Fish

All fish lengths in this paper are standard lengths, in millimeters. Lengths of small fish were determined with the aid of a pair of dividers. Larger fish were measured on a measuring board. Most of the measurements were taken shortly after the fish were caught. When the sample was large, some of the fish were kept temporarily (1 to 2 days) in 10 percent formalin. Preservation in formalin for a week resulted in no perceptible

TABLE 1.—*Number of gizzard shad collected in 1952–55 by methods, year, and month*

[Number of samples in parentheses]

Year and month	Method of collection										Total
	Small-mesh seine[1]	Haul seine	Picked up dead	Experimental gill net	4- or 5-inch mesh gill net	Commercial trap net	Otter trawl	Dynamite	Rotenone	Electric shocking	
1952:											
July	125 (5)										125 (5)
Aug	27 (3)				247 (1)						274 (4)
Sept	9 (2)					17 (2)					26 (4)
Oct	1 (1)										1 (1)
Nov	183 (7)					77 (1)					260 (8)
Dec	92 (6)						390 (2)				482 (8)
1953:											
Jan	24 (3)						7 (1)				31 (4)
Feb			27 (5)								27 (5)
Mar			2 (1)								2 (1)
Apr					1 (1)	324 (17)					325 (18)
May		115 (1)				129 (6)					244 (7)
June	81 (3)	158 (2)									239 (5)
July	1,456 (11)	64 (3)									1,520 (14)
Aug	836 (10)	34 (4)		543 (2)						67 (3)	1,480 (19)
Sept	26 (2)					1,195 (6)					1,221 (8)
Oct	4 (1)			158 (2)		725 (10)					897 (13)
Nov					13 (4)	1,762 (9)					1,775 (13)
Dec					21 (6)	403 (1)	2 (1)				426 (8)
1954:											
Jan			63 (1)		46 (9)						109 (10)
Feb			44 (1)		242 (16)						286 (17)
Mar					20 (7)						20 (7)
Apr					29 (8)	39 (8)					68 (16)
May					18 (7)	63 (11)					81 (18)
June	268 (2)				427 (21)	713 (14)					1,408 (37)
July	143 (9)				227 (8)	540 (16)			650 (2)		1,560 (35)
Aug				94 (2)	120 (7)	77 (2)		7,428 (2)	943 (2)		8,662 (15)
Sept								876 (1)			876 (1)
Oct				132 (1)							132 (1)
Nov											
Dec											
1955:											
Jan					3 (1)						3 (1)
Feb					19 (8)						19 (8)
Mar					2 (1)	2 (1)					4 (2)
Apr					161 (5)	148 (9)					309 (14)
May					6 (3)	204 (12)					210 (15)
June					459 (44)	284 (6)					743 (50)
Total	3,275 (65)	371 (10)	136 (8)	927 (7)	2,061 (157)	6,702 (131)	399 (4)	8,304 (3)	1,593 (4)	67 (3)	23,835 (392)

[1] Of various types mentioned in text.

TABLE 2.—*Gizzard shad collected in 1952–55 by method and locality*

[Number of samples in parentheses]

Locality	Method of collection										Total
	Small-mesh seine[1]	Haul seine	Picked up dead	Experimental gill net	4- or 5-inch-mesh gill net	Commercial trap net	Otter trawl	Dynamite	Rotenone	Electric shocking	
Fishery Bay (South Bass Island, Ohio)	2,350 (38)		126 (7)	927 (7)	1,558 (134)			8,304 (3)	1,593 (4)	67 (3)	14,925 (196)
Bass Islands, Ohio (except Fishery Bay)	27 (1)				316 (21)	6,702 (131)	399 (4)				7,444 (157)
Sandusky Bay, Ohio	76 (4)	371 (10)									447 (14)
Portage River, Ohio	116 (7)										116 (7)
Sandusky River, Ohio	233 (4)										233 (4)
Kelleys Island, Ohio	28 (2)										28 (2)
Pelee Island, Ontario	218 (2)										218 (2)
Green Creek Marsh, Ohio	46 (1)										46 (1)
East Harbor, Ohio	74 (1)										74 (1)
Colchester, Ontario	26 (1)										26 (1)
Long Point, Mich	44 (1)										44 (1)
Point Pelee, Ontario	10 (1)										10 (1)
Avon Lake, Ohio					187 (2)						187 (2)
Mouse Island, Ohio	4 (1)										4 (1)
Maumee Bay, Ohio	23 (1)										23 (1)
Vermilion, Ohio			10 (1)								10 (1)
Total	3,275 (65)	371 (10)	136 (8)	927 (7)	2,061 (157)	6,702 (131)	399 (4)	8,304 (3)	1,593 (4)	67 (3)	23,835 (392)

[1] Of various types mentioned in text.

change in length; and the loss in weight was about percent.

The relation of total length to standard length was obtained by fitting a line by means of least squares to the length measurements. The regression equation was $L_t=4.9+1.23\ L_s$, where L_t is total length and L_s is standard length.

For the determination of age, three or more scales were removed from every gizzard shad longer than 100 mm. Among the smaller shad, scales were taken from random samples of fish from each collection. The scales were placed on a glass slide immediately after removal from the fish, and their annuli counted with the aid of a dissecting microscope. The ages assigned were in terms of the number of annuli. Since the age designation changes on January 1, a fish captured between this date and the actual time of annulus formation was credited with a "virtual annulus" at the edge of the scale (Hile, 1948).

The scales employed in the study of the body-scale relation and for the calculation of growth were removed from a "key area." Since gizzard shad lose their scales readily, a "key scale" frequently would have been missing or regenerated. Use of a key area eliminated discarding shad which lacked the one particular key scale. The key area is on the left side of the fish, just dorsal to a midlateral line and midway between the posterior edge of the operculum and the origin of the dorsal fin. A dozen or so scales from this area were placed in a scale envelope on which was recorded the information pertinent to the fish.

Three nonregenerated scales were taken at random from these key-area scales. For study, they were either impressed on strips of plastic by a cold roller press (Smith, 1954) or mounted dry on glass slides.

The scale measurements were obtained from scale images projected by a microprojection apparatus of the type described by Van Oosten, Deason, and Jobes (1934).

Computations of growth from scale measurements were made nomographically.

Weights are expressed in grams. The largest fish were measured to the nearest gram, fish between 100 and 200 mm. in standard length to the nearest 0.5 g. and those smaller than 100 mm. to the nearest 0.1 g. In catches of large numbers of gizzard shad smaller than 50 mm., those of equal length were weighed en masse and the average weight assigned to each member. Fish preserved for a few days in formalin were sometimes used. Some fish were not weighed when collections were large. Gonads—only from freshly caught shad—were weighed to the nearest 0.01 g.

Ovaries from potential spawners caught in May, June, and July were used for egg counts. From one of the weighed ovaries a small transverse section (1 to 2 g.) was removed and weighed on an analytical balance, its content of current-season eggs counted, and the number of eggs in the entire ovary calculated.

Histological preparations were made of the ovaries of some fish captured in different seasons for studies of oögenesis and ovarian growth and development.

Sex was always determined by dissection except for those fish from which eggs or milt were flowing during the spawning season. When possible, sex was determined for all fish longer than 120 mm. Maturity of males could not be determined in the absence of flowing milt.

SCALE OF THE GIZZARD SHAD

Description of the Scale

The gizzard shad has cycloid scales whose annual growth zones contain many circuli. The relatively closer juxtaposition of the circuli in the first growth zone than in the succeeding zones contributes a darker appearance to this inner portion of the scale. The closely set circuli of this zone are gently arched and, save for those formed earliest, do not curve enough at their ends to reach the transverse groove that separates the anterior and posterior fields but terminate in the lateral fields. This pattern is followed by the circuli of each succeeding growth zone; i.e., the earliest circuli reach the transverse groove, while those produced later terminate laterally. The first circulus of the second growth zone is closely juxtaposed to the last circulus of the preceding zone in the anterior field, cuts across the paths of the later first-zone circuli at their terminations in the lateral fields, and intersects the transverse groove. Thus, it forms roughly a semicircle around the first growth zone. The junction between the first and second growth zones (fig. 2) illustrates one type of demarcation line in the gizzard shad scale. The first annulus of all shad scales examined was of this type. Since this annulus normally is evident only in the lateral fields where the termination of the circuli of the first zone is "cut across" by the circuli of the second zone, it may escape notice under low magnification.

A second type of demarcation line, characterized by a narrow band devoid of clear-cut circuli, normally is found between all growth zones beyond the first. Here, too, the earlier circuli of the more recent zone cut across the paths of the later circuli of the preceding zone in the lateral fields. This type of annulus is clearly evident under low magnification (fig. 3).

Further study is required, but on the basis of my observations I suggest that this second type of annulus is a combination spawning mark and annulus. It is found only on the scales of fish of spawning age. The prominence of this annulus and its possession of a few fragmentary circuli indicate not only a cessation and resumption of growth, but also a period of either poor circulus formation or even of limited scale resorption. Such a period is not indicated by the first annulus. Annulus formation and spawning take place at about the same time (see next section on time of annulus formation). Although no direct causative relation between spawning and annulus formation has been demonstrated, the period of disturbed circulus formation may well be the result of rapid prespawning gonad growth. A few gizzard shad do not spawn during their third year of life (near the start of which the second annulus is formed). These fish may provide the scales on which the second annulus resembles the normal first annulus closely. This type of annulus (fig. 4) lacks the narrow band of fragmentary circuli which makes the usual second and succeeding annuli so conspicuous.

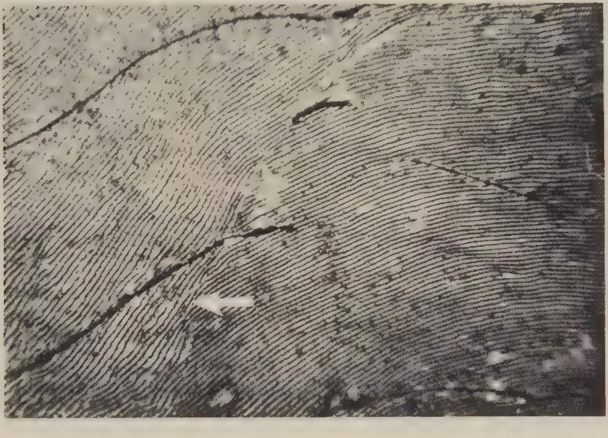

FIGURE 2.—The first annulus of a gizzard shad scale.

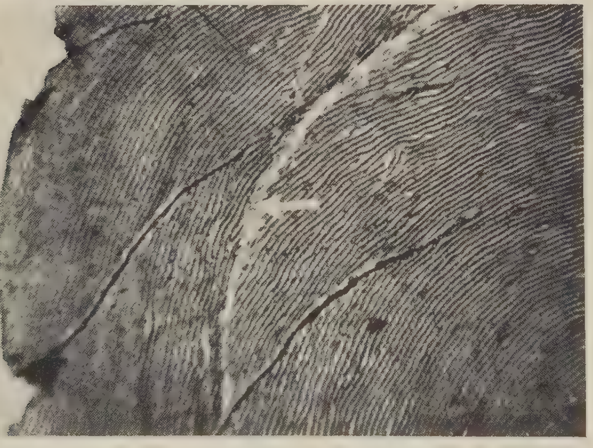

FIGURE 3.—The second annulus of a gizzard shad scale, with clear line between second and third growth zones.

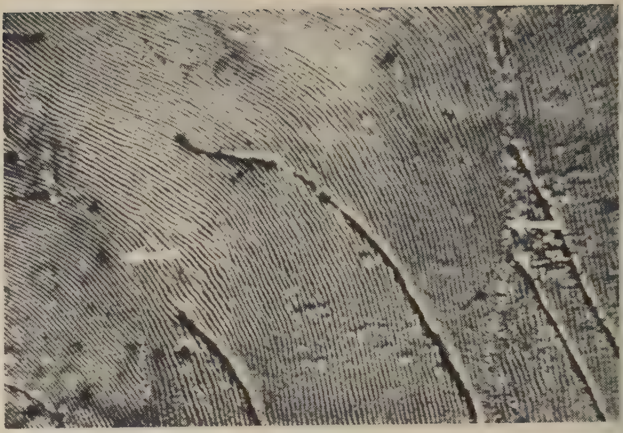

FIGURE 4.—Second annulus of a gizzard shad scale resembling typical first annulus.

Further evidence on the possible effect of spawning on scale structure comes from gizzard shad that show an accessory check between the first and second annuli of their scales (fig. 5); in fact, all accessory checks found were in this position. Fish with this check may be the few shad which spawn during their second year of life. Because the first annulus is already present by the first of June, whereas any precocious second-year spawning occurs in late July—or later in the year (see section on spawning season)—the effect of this late spawning, if it is to be shown by the scale, would have to appear beyond the first annulus.

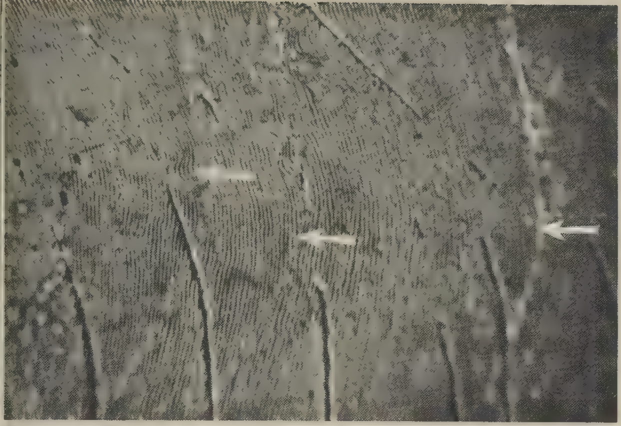

FIGURE 5.—An accessory check on a gizzard shad scale.

Time of Annulus Formation

No new annuli were observed on the scales of any age group of gizzard shad collected in the lake prior to the second quarter of May (table 3). Data for individual days in this second quarter indicated that two of the five males and eight of the nine females of age-group I, taken in the open lake on May 15, had already formed their first annulus. Only one other of the I-group fish, a female captured on May 12, 1955, collected in this quarter had the new annulus. No fish of this age group exhibited annuli in the small collections of May 16–23. (All of the 48 male and 56 female I-group fish caught in Sandusky Bay on May 22, 1953, had their new annulus—data not given in table.) All I-group shad collected after May, however, had completed the new annulus. The new annulus of the II-group fish began to appear in the first quarter of June and the year-mark was present in all of these fish by the first quarter of July. Shad older than the II-group seem to have formed the new annulus about a week later; data for these higher ages, however, are meager. The time of annulus formation, as judged from examination of scales, is in general agreement with the time of resumption of growth in length as indicated by changes in the length of fish (see fig. 8).

Once annulus formation had started, the percentage of females having the new annulus was greater than that of the males until all fish of both sexes had new annuli. On the whole, the female gizzard shad seems to form the annulus as much as a week earlier than the male.

Among the II-group shad, neither length nor weight of either sex was a determining factor in time of annulus formation (a similar study was not made of other age groups). A comparison (made only for June) of the II-group female gizzard shad which had not spawned with those which were spent demonstrated that the percentage of fish having the new annulus was about the same in both groups. Hence, we may assume that the act of spawning neither hastened nor retarded the formation of the new annulus. It may not be concluded, however, that the gonad development which ultimately results in spawning has no effect on the structural appearance of the developing annulus or upon the initiation of a check. Probable evidence of the effect of spawning is seen in the accessory check found between the first and second annuli in the scales of some shad (see previous section on description of the scale).

Validity of the Annulus as a Year-Mark

Lagler and Applegate (1943) and Lagler and Van Meter (1950) demonstrated that the annulus is a true year-mark on scales of gizzard shad in Indiana and Illinois. The following data on shad in Lake Erie add support to the belief that annuli

TABLE 3.—*Percentage of gizzard shad having a new annulus in May, June, and July*

[Combined collections of 1953–55; lake specimens only. Number of fish in parentheses]

Age and sex	Periods in May				Periods in June				Periods in July			
	1–8	9–15	16–23	24–31	1–8	9–15	16–23	24–30	1–8	9–15	16–23	24–31
-group:												
Male	0.0 (51)	9.1 (22)	0.0 (4)	----------	100.0 (10)	----------	100.0 (83)	100.0 (18)	100.0 (50)	100.0 (1)	100.0 (55)	100.0 (21)
Female	.0 (74)	23.7 (38)	.0 (1)	----------	100.0 (8)	----------	100.0 (37)	100.0 (19)	100.0 (75)	100.0 (3)	100.0 (71)	100.0 (20)
I-group:												
Male	.0 (23)	.0 (37)	.0 (23)	0.0 (4)	24.2 (120)	8.4 (166)	52.0 (246)	84.9 (86)	100.0 (29)	100.0 (7)	100.0 (27)	100.0 (2)
Female	.0 (34)	.0 (48)	.0 (37)	----------	32.8 (67)	30.7 (75)	66.4 (125)	96.9 (97)	100.0 (47)	100.0 (13)	100.0 (16)	100.0 (5)
II–VI-group:												
Male	.0 (3)	----------	.0 (6)	.0 (1)	.0 (16)	.0 (26)	.0 (24)	50.0 (2)	75.0 (4)	100.0 (1)	.0 (1)	----------
Female	.0 (3)	.0 (5)	.0 (4)	----------	.0 (5)	.0 (8)	16.1 (31	75.0 (32)	100.0 (26)	95.2 (21)	----------	----------

are valid indicators of age. (Later sections include considerable supporting data on certain of the points.)

1. Gizzard shad known to be young of the year had no annuli on their scales.
2. The scales of these young shad captured in the fall, winter, and early spring showed no annulus at the edge, whereas those taken later exhibited increasing percentages with an annulus until all possessed them.
3. The distance between the last annulus and the scale edge increased through the growing season.
4. Presumed age groups as indicated by modes in length-frequency groupings of shad agreed with groupings based on the number of annuli.
5. The calculated lengths for particular years of life among the age groups of the same and different years of collection agreed with estimates of length from modes of frequency distribution.

Body-Scale Relation

The relation between fish length and scale length in gizzard shad was determined from the "key-area" scales of some 700 fish, ranging in standard length from 43 to 390 mm. A test plotting of the length of the anterior radius (center of focus to anterior edge) of the scale against the standard length of the fish indicated the relation to be linear. The regression line, $L=22.1+44.25\ S$, was fitted by least squares; L=standard length of the fish in mm. and S=anterior radius of the scale in mm. Fish captured in every month and including age-groups I through VI of both sexes are represented in this equation. Studies of the body-scale relation for each sex, for each age group, and during each month revealed no appreciable variation from the general equation.

The empirically derived body-scale equation was the basis for construction of a nomograph for the calculation of growth from scale measurements.

AGE COMPOSITION

Seasonal movements, segregation by size and possibly by maturity, and selectivity of collecting methods complicated the problem of sampling for age composition. The very young gizzard shad of western Lake Erie were found in midsummer close to shore, usually in shallow water. Collecting representative samples of these fish presented difficulties. Capture of the very youngest required the use of dip nets which, of course, the larger fish eluded. As the season progressed and the fish grew larger, Common Sense seines and bag seines were used, but this gear permitted the very smallest fish to pass through the meshes while many of the larger ones escaped capture by their agility and speed. The use of rotenone was selective for the very young shad that could not swim through the poisoned water rapidly enough to avoid being overcome. (Rotenone was used in small areas in the lake with no provisions for holding the fish within the sampling area or for preventing dissipation of the poison into the surrounding waters.) Electrocuting, on the other hand, was selective for the larger shad—the very young ones were unaffected. Finally, I used dynamite. This method proved most successful because fish of all sizes and ages surfaced within the radius of its effectiveness.

As the young gizzard shad become larger (and older) they move into deeper water offshore. By October, the Common Sense seine, which must be fished inshore, will capture some O-group shad but no I-group or older ones; hence, its catches yielded no data on age composition. The gill net captures large O-group shad and also all the older age groups in October, but many smaller O-group shad must pass through the net. Because of these sampling problems, estimates of age composition are unreliable among the 4- to 8-inch shad. Only a few fish of these sizes were captured by experimental gill nets whose meshes ranged from 1 to 4 inches, stretched measure.

Except during the spawning season, gizzard shad older than age-group III were rarely found in the shallower waters. This preference for the deeper water seemed to increase with age.

In view of the segregation by size and the seasonal changes of distribution, small-scale methods of collection could not provide suitably accurate data on age composition. I lacked especially the means to compare data on the 1- to 4-inch group from the shallow waters with records for larger shad from the deeper waters.

Seasonal Changes of Age Composition

Because of the difficulties just outlined, O-group gizzard shad caught by any means other than by trap nets and 4-inch-mesh gill nets have been excluded from this section. The O-group shad in our collection area appear in June, rise to greatest abundance about late July, and diminish in numbers thereafter. Greatest losses occur, presumably, as a result of predation and migration from the collection area.

Although O-group gizzard shad were taken in greatest numbers in late July, none of them had become large enough to be caught by the gill nets and trap nets until August. Subsequently, the size of the collections of the O-group coming into this catchable size range increased regularly until they reached peak abundance toward the end of the calendar year (table 4). They were the dominant age group among fish taken by these nets from August to the end of the year. From January to August of the next year, contrary to expectation, these fish, as the I group, were not dominant in the catch of gill nets and trap nets. Over this period the II-group fish dominated the catches. After August, however, the I group became more plentiful than the older groups and maintained that abundance thereafter.

The scarcity of I-group gizzard shad in the gill net and trap net samples from January to August cannot be fully explained. When all the fish captured in January–July are considered (whether they were obtained by dynamite, rotenone, electrocution—data not tabulated here), then the I group is the dominant group in the collecting area in all the early months except June and July. The June collection especially is noteworthy—the I group was very poorly represented in samples from both the lake and Fishery Bay—especially in the bay where only 4 I-group shad were collected along with 820 II-group fish.

TABLE 4.—*Age composition of gizzard shad taken by trap nets and 4-inch-mesh gill nets, Lake Erie, 1954*

[Percentages of fish in age-groups I–VI given in parentheses—the O-group fish were not considered in the computation of percentages or average age]

Month	Age group							Total and average age [1]
	O	I	II	III	IV	V	VI	
Jan	([2])	4	44	1	-------	-------	-------	49
	-------	(8.2)	(89.8)	(2.0)	-------	-------	-------	1.94
Feb	([2])	12	56	3	2	-------	-------	73
	-------	(16.5)	(76.7)	(4.1)	(2.7)	-------	-------	1.93
Mar	([2])	2	16	5	-------	-------	-------	23
	-------	(8.7)	(69.6)	(21.7)	-------	-------	-------	2.13
Apr	([2])	316	330	36	7	1	-------	690
	-------	(45.8)	(47.8)	(5.2)	(1.0)	(0.1)	-------	1.62
May	([2])	190	187	16	5	1	-------	399
	-------	(47.6)	(46.9)	(4.0)	(1.3)	(.3)	-------	1.60
June	([2])	44	1,656	125	14	2	2	1,843
	-------	(2.4)	(89.9)	(6.8)	(0.8)	(.1)	(0.1)	2.07
July	([2])	287	446	29	4	1	1	768
	-------	(37.4)	(58.1)	(3.8)	(.5)	(.1)	(.1)	1.68
Aug	256	226	27	1	-------	-------	-------	254
	-------	(89.0)	(10.6)	(0.4)	-------	-------	-------	1.11
Sept	899	304	7	1	1	-------	-------	313
	-------	(97.0)	(2.2)	(.4)	(.4)	-------	-------	1.04
Oct	667	221	15	1	-------	-------	-------	237
	-------	(93.2)	(6.3)	(.5)	-------	-------	-------	1.07
Nov	1,686	164	2	-------	-------	-------	-------	166
	-------	(98.8)	(1.2)	-------	-------	-------	-------	1.01
Dec	320	97	5	-------	-------	-------	-------	102
	-------	(95.1)	(4.9)	-------	-------	-------	-------	1.05

[1] Average number of annuli.

[2] Young of the year first became available to the nets in August.

It is noteworthy that the II-group and older shad were taken principally in April through July. Only during the spawning season (June–July) was I able to capture the VI-group shad, which were the oldest in the samples. The August–September samples were dominated overwhelmingly by age group I (89.0 to 98.8 percent). The II group made up 1.2 to 10.6 percent, and only four older fish were taken in the 5 months.

Sampling difficulties, as previously described, prohibited any detailed consideration of fluctuations of year-class strength; however, the 1952 year class apparently was one of unusual abundance. In random samples from commercial trap nets this year class made up 85 percent of the total as age group I, 71 percent as age group II, and 11 percent as age group III.

Survival Rate

Although the records (table 4) do not give a fully satisfactory idea of the age composition of the gizzard shad stock, the collections made in April–July probably permit fairly reliable inference as to the ratios between the numbers in successive age groups for II-group and older shad, since these mature fish seem to constitute a homogeneous group during this period. Collections made from August to December are probably reasonably reliable for determining the ratio of the I-group to the II-group shad. From these two sets of data, I have estimated the survival rate of shad from one age group to the next higher one (table 5).

An estimate (not given in table 5) was made also of the survival of gizzard shad from egg deposition to age-group I. The first step was the calculation, from data on sex ratio (table 15) and fecundity (table 18), of the probable number of eggs deposited by the gizzard shad of age-group II and older. The females of the 6,049 fish (total of the II-group and older of the right-hand column of table 5) were thus estimated to have deposited 926 million eggs. If the 100,000 I-group fish of table 5 are held to be the survivors of this number of eggs (it is assumed that the population is relatively stable), survival from the egg to age-group I is determined as 0.011 percent. This estimate is beset with many uncertainties. It assumes, for example, that the determination of the number of I-group individuals from the ratio of numbers of fish in age-groups I and II in August–November samples was accurate; that year-to-year differences of stock were small enough to justify the pooling of data in the preparation of table 4; that the samples that contributed to table 5 were not unduly biased by gear selection or segregation by size or sex. Even if we granted the survival of 0.011 percent from egg to I-group a wide margin of error, however, the extremely low value still indicates an enormous mortality.

The extraordinarily low survival of the gizzard shad from eggs to the I-group fish probably results from heavy egg and larval mortality, predation, and (in late fall and early winter) buffeting during storms as well as rapid variations in water temperature. When they become the I-group fish, they are usually too large to be eaten by most predatory fish, but they are susceptible to storms and temperature changes that are greatest in waters relatively close to shore where this age group is usually found. As the shad become older, the survival rates improve, probably because the fish tend to remain in the deeper waters where they are less subjected to climatic disturbances.

The oldest gizzard shad that I collected from the western end of Lake Erie in 1952–55 were three of age-group VI (seventh year of life). Patriarche (1953) reported X-group gizzard shad from Lake Wappapello, Mo.

LENGTH-WEIGHT RELATION

General Relation

The mathematical relation between length and weight of gizzard shad captured in western Lake Erie in 1952–55 was determined by fitting the equation $W=cL^n$ to the average empirical lengths and weights of fish in each 10-mm. length interval. The length-weight relation was investigated for each month in which sufficiently large samples were taken. Between mid-1952 and mid-1955 there were 25 such monthly samples. At least one equation was determined for each of the 12 months (for some months adequate samples were acquired in each of the 2 or 3 years—hence, two or three equations). For a month having more than one equation, length and weight data were obtained by each equation, and from these an average monthly length-weight relation was determined. In like manner a "general" length-weight equation was determined from the data calculated by the monthly equations. The sexes were combined for all monthly equations. The general equation was $\log W = -4.81765 + 3.07053 \log L$, where W is the weight in grams and L is the standard length in millimeters.

TABLE 5.—*Survival of gizzard shad from one age group to the next higher one*

[The figures in the first column, body of table, obtained from table 4]

Period of capture and age group	Number of fish	Survivors from 100,000 I group
August–December		
I	1, 012	100, 000
II	56	5, 534
April–July		
II	2, 619	5, 534
III	206	435
IV	30	63
V	5	11
VI	3	6

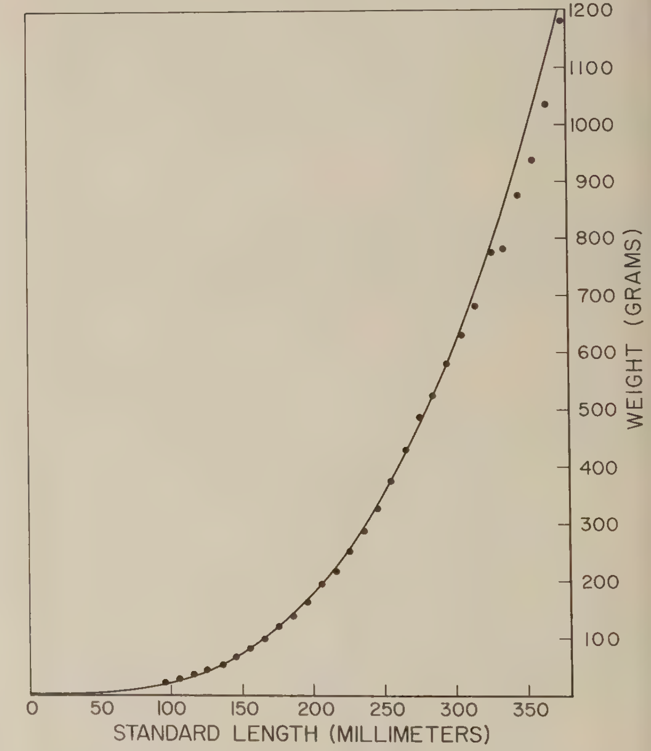

FIGURE 6.—Length-weight relation of gizzard shad in western Lake Erie. The curve is a graph of the general length-weight equation; the data represent the mean empirical values, derived as explained in the text, for the combined collections of 1952–55.

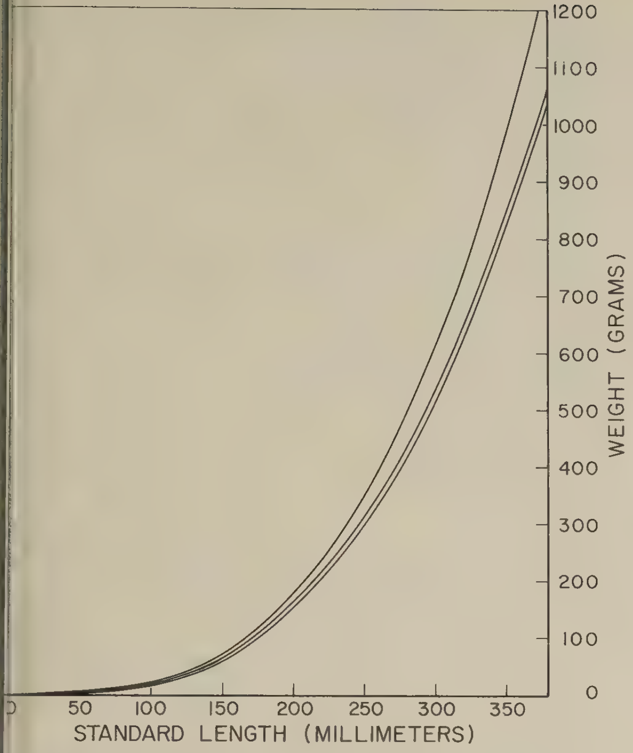

FIGURE 7.—Length-weight curves for gizzard shad from Lake Erie, Missouri, and Illinois. Left curve, Lake Erie; middle curve, Missouri; right curve, Illinois.

Empirical weights and the weights calculated by the general length-weight equation (table 6; fig. 6) agreed well in view of the heterogeneous nature of the materials (records of weight were combined without regard to season, year, sex, maturity, or method of capture). Largest disagreements in measurements concerned the longest fish.

Patriarche and Lowry (1953) determined the length-weight equation to be $\log W = -2.2071 + 2.9812 \log L$ for gizzard shad in the Black River Basin of Missouri. Lagler and Van Meter (1950) reported the equation to be $\log W = -2.2789 + 3.034 \log L$ for shad in Illinois. In both equations, the units are weight in ounces and total length in inches. The curves based on these equations show the Lake Erie shad to be heavier for corresponding lengths than those in Missouri and Illinois (fig. 7).

The weights of male and female gizzard shad were closely similar except in June and July, when the females were consistently heavier than males of corresponding length. This difference frequently has been explained on the basis that the female's ovaries are heavy with eggs soon to be spawned. Although the weight of the ovaries contributes strongly to the heavier total weight of the female gizzard shad, it does not explain it entirely. To investigate this point, the body weight (exclusive of gonad weight) of both sexes should be compared. Unfortunately, I had taken relatively few gonad weights of males—and these over a period of several months which cut across the seasonal changes of weight. However, since the testis weight averaged 1.4 percent of the body weight for these males, I thought I could eliminate the greater part of the weight advantage offered by the ovary by adjusting the female shad's weight to include ovaries weighing only 1 percent of her body weight.

TABLE 6.—*Empirical weights and weights calculated by the general length-weight equation for gizzard shad in western Lake Erie, 1952–55*

Standard length	Weight		Standard length	Weight	
	Empirical	Calculated		Empirical	Calculated
Millimeters	*Grams*	*Grams*	*Millimeters*	*Grams*	*Grams*
20	0.08	0.15	226	251	257
30	.5	.5	236	289	295
40	1.3	1.3	246	328	333
96	20	19	256	373	376
106	26	25	266	428	424
116	35	33	276	484	473
125	43	42	285	525	526
136	54	54	295	581	583
146	67	67	305	629	645
156	82	82	315	680	713
166	99	99	326	776	794
176	118	119	335	781	864
186	138	141	344	876	938
196	161	165	355	937	1,032
206	194	193	365	1,034	1,118
215	215	222	377	1,179	1,234

The adjusted weights of these fish were still greater than those of male shad of corresponding length (table 7). The lesser weight of males may result from their greater activity during the spawning season.

Effect of State of Ovaries on Weight

The study of the effect of the state of development of the ovaries on the weight of the fish was based on records for three categories of fish caught in June 1955: will not spawn, will spawn, and spent.

The gizzard shad that would not have spawned were the heaviest (table 8). The average weight of females which would have spawned was 96 percent of that of the shad which would not have spawned. It appears that the production of mature eggs for spawning reduces the fish's total weight—possibly because some food is stored as

TABLE 7.—*Comparison of weights of male shad at 20-mm. intervals with those of females whose weights have been adjusted to include ovaries of only 1 percent of their body weight*

[Based on June 1955 collection]

Standard length	Weight	
	Males	Females
Millimeters	*Grams*	*Grams*
200	158	189
220	210	244
240	271	309
260	344	383
280	428	467
300	525	563
320	636	669
340	760	788
360	900	919

oil in the eggs rather than as the heavier protein of flesh. The spent fish weighed the least. Their average weight was 85 percent of that of the fish which would not have spawned during the current season. The average percentage loss of weight of mature females at spawning increased with length of fish and averaged 10.7 percent.

Seasonal Differences in the Weight of Fish of a Given Length

The weight of gizzard shad of a given length varies from season to season, and this seasonal variation is similar from year to year. The nature of the seasonal changes (table 9) appears from the average monthly length-weight data. In June and July, when weights of the sexes differed appreciably, the males and females were treated both separately and combined; in other months they were combined.

Gizzard shad attained their greatest weight in August–October, after which the weight declined slowly and irregularly, reaching a low for the combined sexes about May–June. (Interpretations are handicapped by differences of slope in the monthly logarithmic lines.) During the next 2 months, the weights increased rapidly. The weight of the female was least in May (not shown in table 9), and an increase was obvious in June but that of the male reached the lowest point in June.

Studies of the gut contents indicate that gizzard shad consume little food in winter and early spring. During this period they subsist largely on energy stored in the body tissues. Because metabolic rates are low in winter, decrease of the body weight is slight. As the water temperature rises in early spring, the metabolic rate of the fish increases more rapidly than the rate of food intake and the body weight decreases more rapidly. This process gains momentum with the progression of spring until about May–June when the lowest body weight is attained apparently just before the renewed feeding begins to meet the energy requirements of the fish. The occurrence of peak weight, in August–October, undoubtedly is directly related to feeding.

Continued loss of weight in June among the males can be attributed to their spawning activities.

TABLE 8.—*Weights of three groupings of female gizzard shad of different ovarian development, June 1955*

Standard length	Weight of females in category			Loss at spawning
	Would not have spawned	Would have spawned	Spent	
Millimeters	*Grams*	*Grams*	*Grams*	*Percent*
280	510	484	473	2.3
300	610	583	543	6.9
320	722	694	617	11.1
340	846	818	695	15.0
360	982	954	779	18.3

TABLE 9.—*Monthly variations of weight of gizzard shad as determined from the monthly length-weight equations*

WEIGHT

Standard length	January	February	March	April	May	June			July			August	September	October	November	December
						Males	Females	Combined sexes	Males	Females	Combined sexes					
Millimeters	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
200	177	170	179	157	158	161	192	177	186	183	185	198	193	189	181	183
220	240	228	240	215	212	213	249	231	241	242	242	264	256	256	241	245
240	317	298	314	287	277	275	315	295	304	313	309	342	330	336	313	320
260	410	381	402	374	355	348	391	370	377	397	387	435	419	433	398	409
280	519	479	506	478	446	433	478	455	460	494	478	543	521	547	497	514
300	646	593	626	600	551	531	575	553	553	606	580	668	639	680	612	635
320	794	723	764	743	673	642	685	663	658	734	696	810	773	834	742	774
340	963	872	922	907	811	767	807	787	774	878	826	972	924	1,010	890	933
360	1,156	1,039	1,100	1,096	967	908	942	924	902	1,040	971	1,153	1,094	1,209	1,056	1,111

TABLE 10.—*Annual differences of weights of gizzard shad in 1952–55*

[Years compared by pairs; data limited to months for which records are available for both members of the pair]

Standard length	Weights by years									
	1952	1953	1952	1954	1953	1954	1953	1955	1954	1955
Millimeters	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
200	190	186	197	189	172	174	154	169	165	172
220	253	249	264	252	231	237	207	226	223	229
240	330	326	345	326	303	312	272	296	293	297
260	421	416	442	415	389	403	348	379	378	378
280	525	523	555	517	490	510	440	476	478	472
300	650	645	686	636	608	636	546	590	595	581
320	790	787	837	771	744	781	668	720	730	705
340	950	948	1,008	924	898	948	807	869	885	846
360	1,146	1,130	1,204	1,096	1,078	1,138	966	1,036	1,061	1,005
Rating of years	1952>1953		1952>1954		1953<1954		1953<1955		1954>1955	
Months used	Aug., Nov., Dec.		Aug.		Jan., Feb., Apr., May, Aug., Oct.		Feb., Apr., May		Feb., Apr., May, June	

Annual Differences in Weight

The study of the annual differences in the length-weight relation of gizzard shad in 1952–55 was based on data for only those months during which adequate collections were made in at least two of these years. As was brought out in the previous section, the weight of shad varies with the season. Since samples were not adequate for determination of length-weight relations for every month of each year, the use of yearly data would result in a bias in favor of the year during which the specimens were obtained in the months of greatest weight. Consquently, the paired comparisons for 1952–55 were based only on data from months common to both years being compared (table 10).

Shad were heaviest in 1952 and lightest in 1953. The rating of years ran: 1952>1954>1955>1953.

LENGTHS AND WEIGHTS OF AGE GROUPS

The average size of the members of an age group varies with time of capture within the year along clearly seasonal lines. The monthly average lengths of shad show little growth in early spring, rapid growth in summer and early fall, and apparently a cessation of growth in winter for both sexes and all age groups (table 11). The course of growth becomes more apparent when portrayed graphically (fig. 8). After about June of their second year of life female shad were rather consistently longer than males of corresponding age.

The average monthly weights of shad showed, in general, a gradual decrease from the first of the year until June (table 11; fig. 9). This decline was followed by a rapid rise in late summer and fall. Seasonal variation of the length-weight relations (see earlier section) contributed to these changes. The female shad were heavier than males after about June of their second year of life.

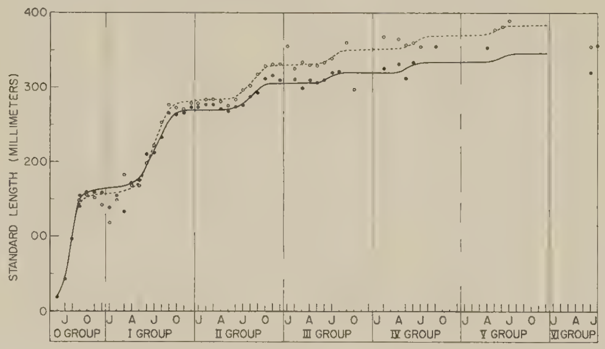

FIGURE 8.—Lengths of gizzard shad at capture in each month by age and sex. Dots are empirical averages of standard length. Open dots represent females; solid dots, males. Curves were drawn by inspection.

The average monthly lengths of the O-group shad warrant special comment. Because some gizzard shad can be found in the spawning state in western Lake Erie from early June to mid-July (see section on length of spawning season), every sample of young shad collected usually contained fish hatched over a period of time, the extremes of which often differed in age by as much as a month or more. The successive collections continually yielded low average changes in length because of the great percentage of the newer, smaller shad constantly added to the population. This bias was aggravated by the tendency of the larger O-group fish to move off-

TABLE 11.—*Average standard lengths and weights of gizzard shad at capture*

Month of capture	O group		I group				II group				III group				IV group				V group				VI group			
	Length	Weight	Length		Weight		Length		Weight		Length		Weight		Length		Weight		Length		Weight		Length		Weight	
			Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
	Mm.	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*
Jan.			133	123	53	42	282	292	503	585		*356		*1,169												
Feb.			*146	129	*69	48	274	283	479	539	314	*305	705	*714	*325	*368	*798	*1,253								
Mar.			*133	*198	*52	*174	280	282	519	515	*298	*334	*574	*865												
Apr.			165	165	85	84	269	279	406	473	308	328	631	835	*324	*364	*678	*1,072	*354		*809					
May			167	160	87	77	267	269	384	411	303	329	540	750	*312	*356	*623	*911		*378		*1,040				
June	18	0.1	195	204	158	188	272	283	396	503	310	333	592	778	333	358	691	926		*382		*1,082	*321	*355	*729	*1,114
July	38	0.7	213	218	232	249	275	294	442	572	320	338	626	854		*355		*1,008		*390		*1,350	*357		*810	
Aug.	61	28	232	241	294	356	285	302	531	687	*313		*636													
Sept.	119	79	258	268	408	446	*303	*317	*568	*722		*360		*1,162	*355		*897									
Oct.	152	84	264	265	441	457	312	330	750	871																
Nov.	152	86	261	269	424	469	*316	*330	*756	*996																
Dec.	138	66	270	273	468	500	*310	*335	*816	*966																

*Asterisk indicates an average based on fewer than five fish.

shore from the sampling area and their growing ability to avoid capture. As a consequence, the sequence of these low average monthly lengths cannot be construed to indicate the rate of growth for these young shad. It was held desirable, therefore, to estimate the position of certain points and of the curve in the preparation of figure 8. No precise quantitative justification can be given for these estimates, but they were based on broad sampling experience and extensive observations on catches in inshore waters. The estimates are held surely to be superior to judgment based on the sadly biased sample records. The curve and points of figure 8 beyond age-group O are based strictly on the records of table 11. The records of monthly growth of table 12 were read from the curve of figure 8.

Gizzard shad of age-group O presumably grew most rapidly in July, August, and September and had peak growth in August. The record for I- and II-group shad indicates that growth in length of the I-group fish progresses rapidly earlier in the year than it does for the II-group. Greatest gain occurred a month earlier—in July. Growth was slight for both groups during May and for the I-group after September.

During the second year of life the male shad grew in length 57 percent as much as during the first year, and in the third year, 28 percent as much. For the female shad the second- and third-year growths were 66 percent and 34 percent, respectively, of the first-year growth.

Seasonal changes in weight resemble those in length (compare figs. 8 and 9) except that weight decreases over winter from the peak attained during the previous fall. The basis for this change was explained earlier in the section on seasonal changes in weight.

Attempts to follow seasonal growth of gizzard shad by use of tagged individuals were unsuccessful. No fish were recaptured from some 600 tagged during the winter of 1952.

CALCULATED GROWTH

Calculated Lengths of Age Groups

The dependability of calculations of length at time of annulus formation is indicated by comparison of the calculated lengths and the lengths of shad which were captured between the end of the growing season and the time of annulus formation (first and last columns of table 13). Because the annuli are the only landmarks on the scale which can be related to a somewhat definite time, and because the shad has practically the same length from the beginning of the calendar year to the time of the annulus formation, the length of a shad captured in this period should agree closely with the length calculated from an older fish to the corresponding annulus.

Agreement was close among adequately represented age groups except for the I-group shad. In the compilation of the empirical data for this group, 105 shad had to be eliminated because sex could not be determined with certainty; their average standard length was 129 mm. Had they been included, the disagreement between empirical and calculated lengths would have been less, but

TABLE 12.—*Progress of season's growth in length of gizzard shad by millimeters and percentage*

[Lengths taken from the curves of figure 8]

	O-group				I-group								II-group							
					Male				Female				Male				Female			
Period	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month
	Mm.	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*
Apr. 30	-----	-----	-----	-----	167	0	0	0	164	0	0	0	263	0	0	0	273	0	0	0
May 30	[1] 5	5	3	3	175	8	8	8	175	11	10	10	266	3	6	6	276	3	5	5
June 30	22	17	13	10	199	24	33	25	204	29	37	27	271	5	17	11	282	6	16	11
July 30	50	28	30	17	225	26	60	27	233	29	64	27	282	11	40	23	294	12	38	22
Aug. 30	114	64	69	39	249	24	85	25	257	24	85	21	297	15	72	32	309	15	65	27
Sept. 30	155	41	94	25	258	9	95	10	268	11	95	10	305	8	89	17	320	11	85	20
Dec. 30	165	10	100	6	263	5	100	5	273	5	100	5	310	5	100	11	328	8	100	15

[1] These fish are assumed to be about a week old. Shad hatched in the laboratory were 3.5 mm. in standard length and became 5.2 mm. long in 4 days.

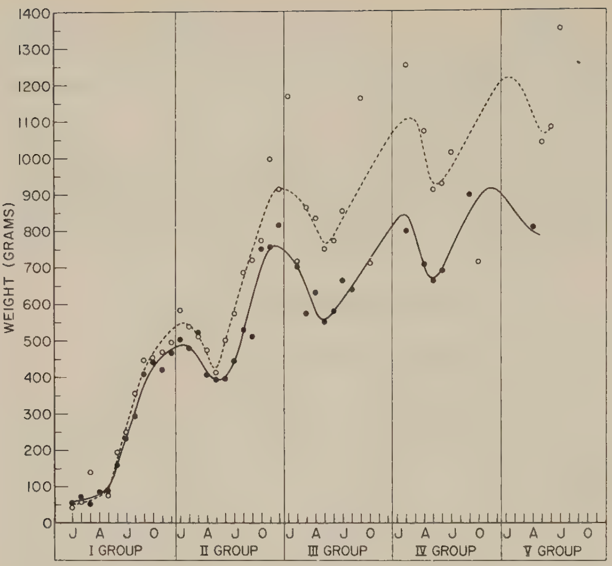

FIGURE 9.—Weights of gizzard shad at capture in each month by age and sex. Dots are empirical averages. Open dots represent females; solid dots, males. Curves were drawn by inspection.

still substantial. The principal cause of the discrepancy was probably the selective sampling of age-group I. Many of this group were too small to be caught by the gill nets and the trap nets. At the higher ages the agreement between empirical and calculated lengths was good. The lengths calculated for each year of life from progressively older shad show a similar close agreement except for the first year of life.

No year classes exhibited consistently fast or slow growth in length, nor did growth appear to have been outstandingly good or bad in any particular calendar year.

Compensatory Growth in Length

It has been observed frequently that although the larger of the young fish maintain a length advantage over the smaller ones during subsequent growth, the smaller young fish grow more rapidly during subsequent years than the larger ones and, thus, reduce progressively the original length difference.

To study this "compensatory growth" in gizzard shad, I tabulated the annual increments of growth of III-group fish, arranged by 20-mm. groupings of length at the end of the first year of life (table 14). The sexes were treated separately, and only fish caught in 1954 were used. In both sexes the annual increments generally varied inversely with first-year length; consequently, the difference in length between the shortest and the longest first-year fish diminished progressively to a minimum in the third year.

TABLE 13.—*Comparison of the average empirical standard length of gizzard shad with average length calculated for each year of life for each age group for each sex*

[Fish of the same age were combined without regard for year classes. Empirical lengths are given only for shad captured between the end of the growing season and the time of annulus formation. Number of fish in parentheses]

Sex and year of life	Average empirical length	Age group					Average calculated lengths [1]
		I	II	III	IV	V	
Male:	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm*	*Mm.*
First	165	146	130	145	146	139	141
	(227)	(76)	(92)	(34)	(8)	(2)	
Second	273	------	270	282	270	270	273
	(530)	------	(37)	(34)	(8)	(2)	
Third	313	------	------	316	312	310	313
	(53)	------	------	(5)	(8)	(2)	
Fourth	328	------	------	------	348	337	343
	(8)	------	------	------	(1)	(2)	
Fifth	350	------	------	------	------	349	349
	(1)	------	------	------	------	(1)	
Females:							
First	162	134	139	146	144	138	140
	(267)	(71)	(118)	(62)	(13)	(3)	
Second	283	------	285	292	280	282	285
	(489)	------	(57)	(62)	(13)	(3)	
Third	335	------	------	336	333	336	335
	(83)	------	------	(42)	(13)	(3)	
Fourth	361	------	------	------	362	369	366
	(17)	------	------	------	(6)	(3)	
Fifth	383	------	------	------	------	390	390
	(4)	------	------	------	------	(1)	

[1] Unweighted means.

TABLE 14.—*Average annual increments of length of III-group shad of the 1954 collections arranged by 20-mm. groups of first-year calculated length*

[Second- and third-year calculated lengths given in parentheses]

Males				Females			
Number of fish	First year	Second year	Third year	Number of fish	First year	Second year	Third year
	Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*
1	96	161	49	--------	--------	--------	--------
	--------	(257)	(306)	--------	--------	--------	--------
4	109	162	36	9	114	169	50
	--------	(271)	(307)	--------	--------	(283)	(333)
10	132	151	31	12	131	160	45
	--------	(283)	(314)	--------	--------	(291)	(336)
10	154	131	28	22	152	139	43
	--------	(285)	(313)	--------	--------	(291)	(334)
3	173	114	31	13	166	135	38
	--------	(287)	(318)	--------	--------	(301)	(339)
4	185	105	25	3	184	124	36
	--------	(290)	(315)	--------	--------	(308)	(344)
Difference in standard length [1]	89	33	9	--------	70	25	11
Difference in length increments [1]	--------	56	24	--------	--------	45	14

[1] Between shortest and longest first-year groups.

REPRODUCTION AND EARLY DEVELOPMENT

ze and Age at Maturity

The sex and maturity of gizzard shad were
ways determined by dissection except for those
sh from which eggs or milt were flowing during
e spawning season. Vladykov (1945) stated
at the males have darker fins than the females,
ut I found that neither this nor any other readily
iscernible external characteristic indicated the
x with reasonable consistency for all age groups
all seasons. Generally, however, one might
xpect a shad that is relatively deep for its length
be a female. Since the time of this study,
oen (1959) sexed gizzard shad by examining
e urogenital opening with a probe.

The sex of large fish was determined easily—
e testes were opaque white, whereas, the ovaries
ere mostly semitranslucent and light yellow or
ink. Sex determination was more difficult in
nall shad. Here, the testes were whitish and
e ovaries almost colorless and translucent, but
e distinction between them became less and less
pparent as one examined smaller and smaller
onads. After much study (comparisons of judg-
ents from macroscopic examination with subse-
uent determinations from histological sections) I
ould frequently distinguish the sexes macroscopi-
ally when the diameter of the gonad was only 1
m. and readily when it attained 2 mm. The
inimum standard length of fish for which sex
ould be determined macroscopically with confi-
ence was about 120 mm. (4 or 5 months old),
lthough on occasion sex could not be determined
r a larger shad.

Although a fish whose milt or spawn flows
uring the spawning season is sexually mature,
he absence of this feature does not indicate im-
aturity. In this situation, during the spawning
eason or any other time, different criteria must
e employed. Histological studies of ovaries
ollected throughout the year have enabled me
o recognize a potential spawner several months
n advance of the spawning season and spent fe-
ales as long as a month after spawning. More-
ver, the relation of the histological characteristics
f the ovary to the gross appearance of that organ
ade possible an estimate of maturity by gross
bservations. In females that will not spawn, the
varies contain only minute, scarcely visible eggs,
whereas potential spawners exhibit, in addition to the minute eggs, fair-sized ones that are clearly visible within the semitranslucent ovary several months prior to spawning. Although completely spent females have only the minute eggs that are characteristic of the ovaries of fish which will not spawn, their ovaries for a few weeks after spawning are more flaccid than those of nonspawners, the minute eggs are some little distance apart, and the interovular spaces have a more watery appearance.

The maturity of males could not be determined in the absence of flowing milt. The presence of motile sperm, obtained by lancing a testis, does not assure maturity. Males examined in January had motile sperm—even the I-group males, most of which would not spawn in the spring. Maturity in males is undoubtedly associated with structural development or physiological change which permits release of the sperm. The great scarcity of I-group males at the spawning site in May and June suggests that this release mechanism does not usually become functional in males of that age. The presence of a few of them on the spawning grounds during July may indicate that some have matured near the end of the spawning season.

In 1954, I found three mature I-group female shad. Their standard lengths were 197, 225, and 236 mm. Some 25 or 30 I-group males, 190 to 230 mm. long, also were mature. The milt and spawn produced by fish of this age were scanty. The crosssection of an ovary of a mature I-group female reveals few mature eggs (fig. 10).

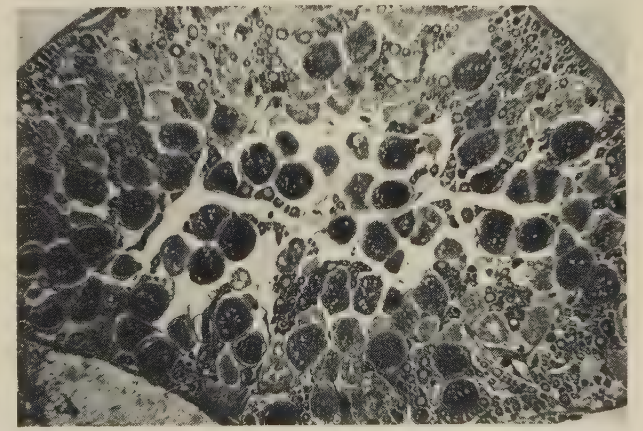

FIGURE 10.—Cross section of an ovary of a mature I-group gizzard shad showing relatively few near-mature eggs (July 6, 1954).

Invariably, these precocious fish arrived at the spawning site in July, near the end of the spawning season. They were not the largest of their age group, whose length range extended to 254 mm. at this time, but were generally above the average length. They obviously represented only a fraction of their group, but the exact percentage could not be determined because segregation according to maturity is great during the spawning season.

Most spawners were in their third year of life (II group), but not all shad of this age group spawned. The average length of the June 1954 II-group females that would have spawned (29 cm.) was 1 cm. greater than that of the shad which would not have spawned during the current year (28 cm.). Although the percentage of the female shad that matured during their third year of life could not be determined because of the segregation according to maturity, observations on gonads of shad captured throughout the year indicated that at least 80 percent of them became mature at this age in western Lake Erie. Only rarely were female shad older than the II-group immature. With few exceptions, the II-group male shad had well-developed testes. Since, however, I was unable to determine maturity in the absence of flowing milt, I could not distinguish a spent individual from one which had not spawned—in fact, could not judge from the state of the testes in any month the percentage of mature males of any age group.

Table 15.—*Sex ratios for gizzard shad for which both sex and age were determined monthly*

[These shad were captured in the vicinity of the Bass Islands in 1952–55]

Month and sex	Age group							Total for month
	O	I	II	III	IV	V	VI	
January:								
Male	------	7	14	------	------	------	------	21
Female	------	7	31	1	------	------	------	39
Percentage males	------	50.0	31.1	0.0	------	------	------	35.0
February:								
Male	------	8	135	5	2	------	------	150
Female	------	15	104	3	1	------	------	123
Percentage males	------	31.8	56.5	62.5	66.7	------	------	54.9
March:								
Male	------	1	5	3	------	------	------	9
Female	------	2	10	2	------	------	------	14
Percentage males	------	33.3	33.3	60.0	------	------	------	39.1
April:								
Male	------	151	156	17	3	1	------	328
Female	------	177	164	16	4	------	------	361
Percentage males	------	46.0	48.8	51.6	42.9	100.0	------	47.6
May:								
Male	------	48	90	8	4	------	------	150
Female	------	69	128	7	3	1	------	208
Percentage males	------	41.0	41.3	53.3	57.1	0.0	------	41.9
June:								
Male	------	21	913	65	4	------	1	1,004
Female	------	21	753	62	10	2	1	849
Percentage males	------	50.0	54.8	51.2	28.6	0.0	50.0	54.2
July:								
Male	------	121	172	5	------	------	1	299
Female	------	166	315	24	4	1	------	510
Percentage males	------	42.2	35.3	17.2	0.0	0.0	100.0	37.0
August:								
Male	119	104	13	1	------	------	------	237
Female	116	100	13	------	------	------	------	229
Percentage males	50.6	51.0	50.0	100.0	------	------	------	50.9
September:								
Male	410	118	4	1	1	------	------	534
Female	516	159	3	------	------	------	------	678
Percentage males	44.3	42.6	57.1	100.0	100.0	------	------	44.1
October:								
Male	319	123	9	------	------	------	------	451
Female	352	99	6	1	------	------	------	458
Percentage males	47.5	55.4	60.0	0.0	------	------	------	49.6
November:								
Male	827	73	1	------	------	------	------	901
Female	876	92	1	------	------	------	------	969
Percentage males	48.6	44.2	50.0	------	------	------	------	48.2
December:								
Male	221	37	1	------	------	------	------	259
Female	276	60	4	------	------	------	------	340
Percentage males	44.5	38.1	20.0	------	------	------	------	43.2
Total in age groups:								
Male	1,896	812	1,513	105	14	1	2	4,343
Female	2,136	967	1,532	116	22	4	1	4,778
Percentage males	47.0	45.6	49.7	47.5	38.9	20.0	66.7	47.6

Sex Ratio

The gizzard shad captured in the vicinity of the Bass Islands in 1952–55 for which sex could be determined were combined to show trends of the sex ratio by month and by age (table 15).

Only limited seasonal trends are apparent from the data on sex ratio; the month-to-month fluctuations were decidedly irregular.

Among the 10 months in which the total samples exceeded 250 fish, July stands apart because of the small percentage of males (37.0 percent). Among the other 9 months, this percentage ranged between 41.9 (May) and 54.9 (February). The percentage for all 12 months was 47.6.

The percentage of males varied little among the four younger age groups (45.6–49.7 percent males) in the combined sample for all months, but males became less numerous at the higher ages (38.6 percent in age groups IV–VI, combined).

Information on the percentage of males in samples from the shallow waters of Fishery Bay and the deeper waters of the lake gives no indication of segregation of the sexes within the lake except for age groups II and III (shad of spawning age) during June. The records for that month (table 16) suggest that males are relatively more plentiful at the spawning site than in the deeper water. The data on sex ratio on the spawning site during the spawning season are undoubtedly biased in favor of the males since their greater activity increases the likelihood of capture by the stationary fishing gear. This bias, however, does not account entirely for the large percentage of males

TABLE 16.—*Sex ratios for gizzard shad caught in the shallow waters of Fishery Bay and in the deeper waters of Lake Erie for June and for all other months combined in 1952–55*

Month and site of capture	Sex	Age group							Total
		0	I	II	III	IV	V	VI	
June:									
Bay	Male		5	610	47	3			665
Do	Female		6	207	16				229
Do	Percentage males		45.6	74.7	74.6	100.0			74.4
Lake	Male		16	303	18	4		1	342
Do	Female		15	546	46	10	2	1	620
Do	Percentage males		51.6	35.7	28.1	28.6	0.0	50.0	35.6
All months except June:									
Bay	Male	63	214	154	6	1			438
Do	Female	82	207	196	6	2			493
Do	Percentage males	43.4	50.8	44.0	50.0	33.3			47.0
Lake	Male	1,833	577	446	34	6	1	1	2,898
Do	Female	2,054	739	583	48	10	2		3,436
Do	Percentage males	47.2	43.8	43.3	41.5	37.5	33.3	100.0	45.8

on the spawning site; in the deeper waters the percentage of males is greater between spawnings than during the spawning season.

The sex ratios of mature shad captured in Fishery Bay and in the deeper waters of the lake within 7- or 8-day periods in May, June and July of 1954 and 1955 (table 17) indicate that the percentage of males in the population of shad captured in the bay increased during early and mid-June and reached a high in the third quarter; the females were relatively most numerous in the last quarter. Males were scarce in deeper water in June (exception, June 9–15), and with the exception of one sample (July 16–23), this scarcity continued through July. Data are few on the sex ratio in Fishery Bay in July; females predominated strongly in the single sample. The generally small percentages of males in all July samples account for the low monthly percentage for July, mentioned in the earlier description of table 15.

TABLE 17.—*Sex ratios for mature gizzard shad captured in the shallow waters of Fishery Bay and the deeper waters of Lake Erie during May, June, and July, 1954 and 1955*

Time of capture	Bay			Lake		
	Male	Female	Males	Male	Female	Males
May:	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
1–8	1	1	50.0	23	32	41.8
9–15	5	7	41.7	29	44	39.7
16–23	1	2	33.3	28	39	41.8
24–31	5	0	100.0			
1–31	12	10	45.5	80	115	41.0
June:						
1–8	135	52	72.2			
9–15	142	48	74.7	49	34	59.0
16–23	261	42	86.1	96	247	28.0
24–30	122	82	59.8	181	346	34.1
1–30	660	224	74.7	326	627	34.2
July:						
1–8	58	95	37.9	84	170	33.1
9–15				8	15	34.8
16–23				23	14	62.2
24–31				2	5	28.6
1–31	58	85	37.9	117	204	36.4

DEVELOPMENT AND MATURATION OF THE EGG

For convenience in description, the development of the egg has been divided arbitrarily into six stages (fig. 11). The following descriptions were made from ovary sections fixed in Bouin's solution and stained with hematoxylin and eosin.

Stage 1.—The young oöcyte is 10 to 20 μ in diameter and has a large nucleus with a centrally located nucleolus. The nucleolus and nuclear membrane stain darkly with the hematoxylin, while the cytoplasm and the nucleoplasm stain with eosin.

Stage 2.—The oöcyte, now 20 to 70 μ in diameter, has not yet acquired its follicle-cell envelopment. The nucleus has grown at a faster rate than the cytoplasm. This cytoplasm is now accepting some of the hematoxylin, while the ground substance of the nucleus still stains with eosin. The nucleolus, if present, is lost among the darkly staining chromatin materials which are somewhat scattered throughout the nucleus.

Stage 3.—This stage includes oöcytes which range from 0.07 mm. to 0.15 mm. in diameter. The nucleus and cytoplasm appear to have grown at the same rate from the last stage. The cytoplasm now stains darkly with hematoxylin; the nuclear sap stains pink. The dark-staining chromatin material is more plentiful and is arranged circumferentially along the periphery of the nucleus. Flat follicle cells are arranged as a single-celled layer around the oöcyte.

Stage 4.—The follicle is mostly in the 0.15-to 0.30-mm. size range in this stage. The dark-staining cytoplasm is growing more rapidly than the nucleus. As the follicle approaches the 0.30-

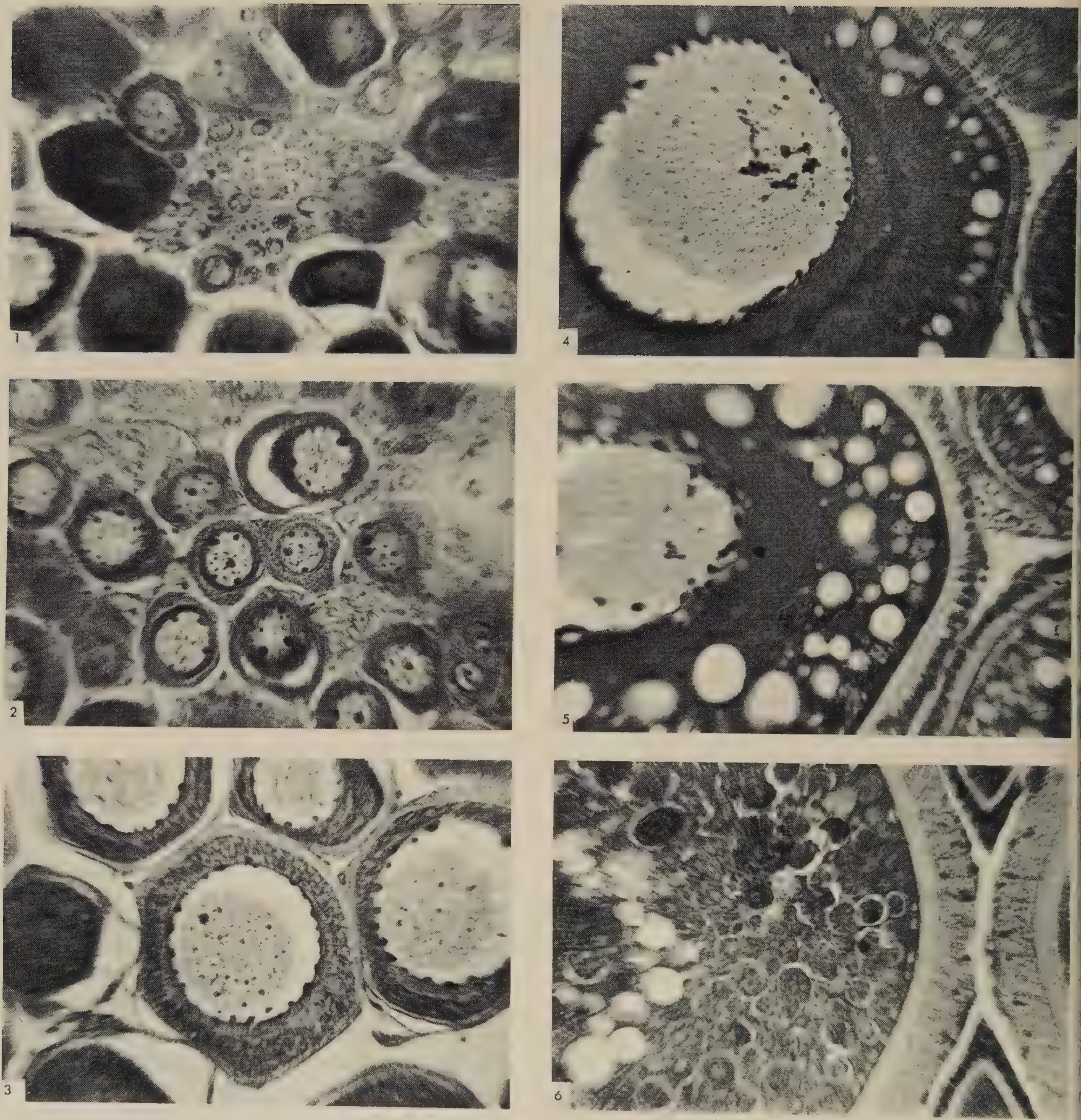

Figure 11.—Growth and maturation of gizzard shad eggs.

mm. size, the oöcyte's cytoplasm is stained by both hematoxylin and eosin—the resulting reddish-purple oöcyte is clearly noticeable among the bluish-purple smaller oöcytes. The nuclear membrane and chromatin material surrounding the pink-staining nucleoplasm appear fuzzy as though disintegrating. Oil globules have formed in the periphery of the cytoplasm beneath the follicle cells that have become cuboidal.

Stage 5.—In this stage the oöcyte with its envelope of follicle cells—now columnar—grows from 0.30 mm. to about 0.45 mm. The nuclear membrane has largely disintegrated, and chromatin material has all but lost its discreteness.

The peripherally formed oil globules have become larger and are moving toward the nuclear area. Small yolk granules have appeared, some of which have encroached upon the nuclear area, making this area smaller than it was in the preceding stage. These yolk granules stain mostly with eosin, while the cytoplasmic ground substance stains with both dyes. A homogeneous vitelline membrane has made its appearance between the oöcyte and its surrounding follicle layer.

Stage 6.—During this stage the follicle size is between 0.45 mm. and 0.50 mm. The nuclear membrane and chromatin material are no longer evident; the oil globules have migrated around the nuclear area and encroached upon it so that the area now is relatively small. During this migration, the yolk granules have moved away from the central area, leaving this area surrounded by oil globules. The small yolk granules of the previous stage have now become very coarse. The vitelline membrane under the single-celled follicle layer is now thick and prominent.

Up to this stage the oöcyte appeared to be isolecithal since the nucleus occupied a central position as long as it was evident and the amount of yolk compared with the size of the nucleus did not seem to be plentiful. Just prior to spawning, however, the oil globules almost completely disappear and the cell is so packed with large yolk granules that no definite nuclear region is recognizable. The tremendous amount of yolk, despite the lack of information regarding the location of the nucleus, suggests that the oöcyte now is telolecithal.

Before the egg leaves the ovary, the single-celled follicular layer ruptures and separates from the vitelline membrane. The former remains in the ovary where it gradually disintegrates. The vitelline membrane becomes greatly distended by imbibed water after the egg is spawned and water-hardened.

Most of the O-group gizzard shad already had oöcytes in Stages 1 and 2 as early as October. After they appeared, they were a constant feature in the ovary; they were most abundant in the fall in O-group fish, somewhat less abundant in older fish immediately after spawning, and least plentiful in ripe fish. In the O-group shad the oöcytes begin development so late in the season that usually they do not progress beyond Stage 2 by late fall; there is an accumulation of Stages 1 and 2. Older shad which spawned, however, showed no such accumulation, for the oöcytes that formed earliest had time to progress to later stages. Their constant presence—though they are not plentiful in near-ripe and ripe fish—indicates that one or both of the following processes must occur: these early stages are continually being formed, perhaps at varying rates; or the oöcytes formed later in the generative season—if there be one—remained more or less dormant throughout the remainder of the season—the nutrients being diverted to the earlier formed, more advanced oöcytes.

In shad which had spawned, oöcytes in Stages 3 and 4 are found in late fall and winter, but in the youngest shad (I group after January) they appear in spring.

Stages 5 and 6 usually do not appear in the I-group fish; they are present in spring in the II-group shad, and are found in spring and early summer in the older females.

SEASONAL CHANGES IN THE OVARY

The seasonal changes in the ovary of every gizzard shad are much the same after the first spawning, which occurs usually in II-group fish. Changes preliminary to first spawning follow a different course.

During fall, the oöcytes of O-group fish appear late and progress so slowly that by the time the spawning season arrives (fish are now I-group) the eggs are not mature enough to be spawned. In a few fish of this age (presumably those which hatched very early) some of the eggs become mature and are spawned late in the spawning season (fig. 10). In a few others, the eggs become mature too late to be spawned and are resorbed (fig. 12). In most of these I-group fish, however, most of the eggs have developed to Stage 4 (fig. 11), and remain at that stage until the next spawning season approaches.

For convenience, the ovarian changes of gizzard shad after their first spawning have been divided into six stages (fig. 13).

Stage A.—In late July, August, and early September, the shrunken ovary is filled with oöcytes in Stages 1, 2, and 3. The germinal epithelium extends inward from the periphery of the ovary in irregular layers. The central cavity of the saccular ovary is highly variable and is much branched. The branches extend between the layers of the germinal epithelium.

Stage B.—From late September to early November the ovary contains a greater proportion of oöcytes in Stage 3 than earlier in the season. Some oöcytes of Stage 4 are also present.

Stage C.—During winter and early spring the ovary contains some oöcytes in Stage 5, a great many in Stage 4, and decreasing numbers in the earlier stages.

Stage D.—In April, May, and early June the ovary has oöcytes mostly in Stages 5 and 6; those in Stage 6 become more and more predominant toward the close of this period. Some oöcytes in Stages 1 and 2 also are present. Those in Stages 3 and 4 are rare. The central cavity of the ovary is obliterated by the dense packing of the large oöcytes.

Stage E.—In June, the eggs in the ovary are in a stage subsequent to the last stage shown in figure 11—some are ready to be spawned. That others have left the ovary is apparent from the empty spaces and the follicular remnants. Oöcytes in Stages 1 and 2 are present—a few in Stages 5 and 6 may still be found.

Stage F.—Immediately after spawning and perhaps for a week or two later the ovary contains remnants of the old follicular layers. The oöcytes present are mostly in Stages 1 and 2, but some have already reached Stage 3.

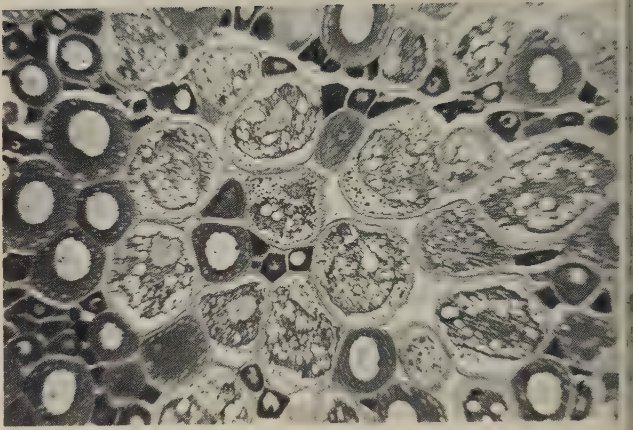

FIGURE 12.—Unspawned eggs being absorbed while new eggs are developing (I-group gizzard shad, December 16, 1953).

The seasonal progression of ovarian change by no means proceeds at the same rate in all gizzard shad. The figures represent the situation for most shad in western Lake Erie. In some of the fish the stages are months in advance of those given in the figure; in others, they are months tardy. Nevertheless, differences among individuals decrease as the spawning season approaches. Fish with advanced rates exhibit slower development just prior to the spawning season, but development proceeds rapidly in fish with retarded rates.

Fecundity

The number of eggs per individual varied considerably (table 18). Although the number of counts is meager, the averages for the age groups definitely show low egg production among the precocious I-group shad, a maximum production by the II-group fish, and slowly declining numbers among successively older age groups.

TABLE 18.—*Number of eggs per individual gizzard shad of different sizes and ages*

Age and date of capture	Standard length	Weight	Ovary weight	Estimated eggs per fish	Eggs per gram of fish	Eggs per gram of ovary	Ovary as percentage of fish weight
	Mm.	*G.*	*G.*	*Number*	*Number*	*Number*	*Percent*
Age group I:							
July 6, 1954	225	260	3.9	22,400	86	5,744	1.5
July 8, 1954	236	305	14.8	96,560	317	6,524	4.8
Average	231	283	9.4	59,480	210	6,328	3.3
Age group II:							
May 23, 1955	282	524	78.6	543,910	1,038	6,920	15.0
June 3, 1954	285	529	71.7	524,580	992	7,316	13.6
May 20, 1954	292	593	35.2	211,380	356	6,005	5.9
May 20, 1954	293	578	24.6	258,350	447	10,502	4.3
May 23, 1955	305	526	55.8	356,710	678	6,393	10.6
Average	291	550	53.2	378,990	689	7,124	9.7
Age group III:							
May 23, 1955	322	713	44.5	406,170	570	9,128	6.2
June 18, 1954	328	700	62.6	367,670	525	5,873	8.9
June 24, 1954	343	847	36.2	260,510	308	7,196	4.3
Average	331	753	47.8	344,780	458	7,213	6.4
Age group IV:							
June 18, 1954	348	882	28.8	267,220	303	9,278	3.3
June 23, 1954	363	895	74.2	350,280	391	4,721	8.3
Average	356	889	51.5	308,750	347	5,995	5.7
Age group VI:							
June 23, 1954	355	1,114	29.8	215,330	193	7,226	2.7

As the fish become older, their ovaries acquire increasing amounts of connective tissue; hence, they should produce fewer eggs per gram of ovary with increase in age. This anticipated change is not borne out, however, in table 18. The per-gram-ovary yield of eggs was highly variable, even among the fish of an age group. The situation is not surprising since the problem of finding differences is compounded by the fact that the ovaries were in varying stages of development at the time the fish were captured. An ovary contains a certain number of eggs which would be spawned during the coming spawning season. These eggs, together with immature ones and other components of the ovary, make up the weight of the ovary. The farther along these eggs develop the heavier they become; the weight of the ovary increases and its per-gram yield of eggs decreases.

On the per-gram-of-fish basis the older fish do, indeed, produce fewer eggs than the younger ones (except the precocious I group). The "relative fecundity" tripled from the I group to the II group and then declined to age-group VI which had about the same value as the I group.

On the basis of fish size it would appear that fish weighing 500–600 g. produce more eggs than do those whose weights fall either below or above that range. The productivity of these fish may be the result of age rather than size, however; in the table only the II-group shad occupy this range. Further information on this possibility was gained from 69 II-group female shad, captured in the first two quarters of June 1954; their weights ranged from 339 to 733 g. They were divided by 50-g. groupings (301 to 350, 351 to 400, —), and the ratio of ovary weight to fish weight was calculated for each group. (Egg counts had not been made on these fish.) The ratio was highest for the 500- to 600-g. fish. This finding would suggest, then, that fish in this weight range produce the most eggs.

Spawning

The single spawning site of gizzard shad that I was able to find was a bar some 200 feet long and covered by 2 to 4 feet of water near Put-in-Bay. The bottom is topped with sand, gravel, and boulders. *Cladophora*, *Myriophyllum*, and *Butomus umbellatus* (forma *vallisneriifolius*) are abundant during the spawning season.

No gizzard shad were found on this bar in 1954 prior to, or after, the spawning season. To learn the day-to-day variations of the numbers of shad there during the 1955 spawning season, I set a 100-foot, 4-inch-mesh gill net nightly along the top of the bar from May 9 to June 30. The catches, together with the water temperatures, are recorded in table 19.

It was evident later that the female shad does not spawn her entire egg holdings in one visit to the bar. Consequently, some shad would probably have visited the bar more than once during the season had they not been caught. Furthermore, gizzard shad exhibit greater activity at the height of spawning than just prior to it or afterwards. Hence, greater percentages of those present in a given area are likely to swim afoul of the net at this time than at other periods. The table must be interpreted with these points in mind.

Temperature clearly is important in the onset and progress of spawning. Gizzard shad first appeared in the net on this bar at a temperature of 59° F. and were common at about 67° F. Indeed, when the water temperature dropped slightly (to 65° and 65.5° F. on June 12–15) the numbers of shad also dropped.

To define the spawning site more precisely, I set gill nets transversely across the bar. In every

TABLE 19.—*Water temperatures and daily captures of shad by a 100-foot, 4-inch-mesh gill net set on a spawning site in Fishery Bay in May and June 1955*

[The net was lifted daily at 9 a.m. except on June 2–11 (see text); the water temperature was read at the time of lifting]

Date	Shad caught	Water temperature	Date	Shad caught	Water temperature
	Number	*° F.*		*Number*	*° F.*
May 10	------	58.0	June 5	12	66.0
11	------	59.0	6	21	67.5
12	------	58.5	7	23	66.5
13	------	60.0	8	24	65.5
14	------	60.0	9	5	66.5
15	------	59.0	10	10	66.5
16	------	61.5	11	16	66.0
17	------	59.5	12	6	65.5
18	------	59.0	13	4	65.0
19	1	59.0	14	1	65.5
20	------	60.0	15	1	65.5
21	------	61.0	16	14	68.0
22	------	61.0	17	57	70.0
23	------	61.0	18	35	71.0
24	------	61.0	19	38	71.5
25	------	61.5	20	20	72.0
26	------	61.0	21	10	71.0
27	------	62.5	22	10	71.5
28	------	63.0	23	4	72.0
29	1	63.0	24	33	72.5
30	------	62.0	25	24	73.0
31	------	63.0	26	5	73.0
June 1	4	64.0	27	10	74.0
2	6	65.5	28	5	73.5
3	20	67.0	29	18	73.5
4	10	66.0	30	17	73.0

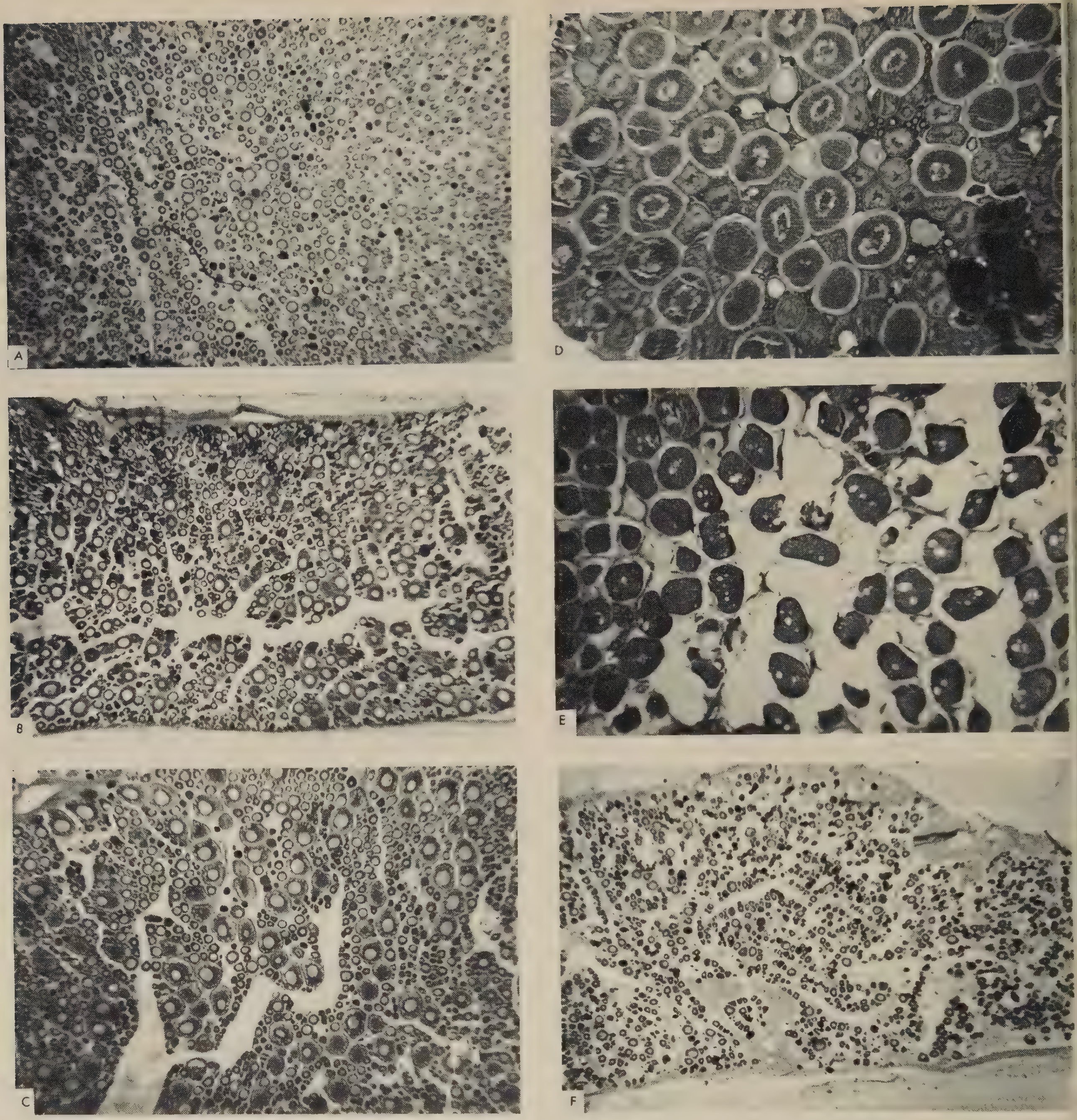

FIGURE 13.—Six stages in the seasonal changes in the ovary of gizzard shad.

lift most of the gizzard shad were caught in that portion of the net that crossed the highest area of the bar, and fewer at the ends of the nets where they sloped gradually into deeper water.

The conditions described here must not be taken as the only ones under which gizzard shad may spawn. Although I have little information on possible shad spawning in the lake, and have never taken shad eggs in plankton nets in the open lake, gill nets and trap nets sometimes have had eggs of gizzard shad and other fish adhering to them during the spawning season. The females may have forced spawn from themselves during their attempts to escape from the gill nets or they ay have been held beyond their spawning time the trap nets, which were lifted only every ther day.

It is also probable that some gizzard shad are ot able to find a suitable spawning site by the me the eggs are ready to be expelled. This ossibility is supported by the observation that ome of the female shad caught in the lake by ommercial fishermen were releasing eggs. To xplore this possibility further, I determined the ercentage of spawning fish for the II–group and lder female shad caught in Fishery Bay and for hose captured in the lake during May, June, and uly 1954–55 (table 20). The state of the ovaries as determined by gross examinations. The uch smaller percentages of spawning shad cap- ured in the lake than in the bay suggest that most f the ripe females migrated from deeper to shal- ower water during the spawning season. This nding is not in disagreement with the earlier bservation (tables 16 and 17) that the percentage f females in June was less in the shoal water than the deeper water. The high percentage of males n the spawning reef can be explained on one r more of the logical assumptions that: greater umbers of males than females entered the shoal rea from the lake; that activity was greater mong the males than among the females in the hoal waters; that males individually stayed longer the site.

When fish begin to spawn, the rise in the spawning" category should coincide with the rop in the "nonspawning" category if the fish o not migrate from the area. Lack of this relation in the lake provides further evidence that most of the fish do not remain in the deeper water when they are ready to spawn.

The rapid rise of the "spent" category in the lake from mid-June through July, which is completely out of proportion with the drop in the "spawning" group there, indicates a return of the spent fish from shallow water to the open lake.

The data of table 20 on the percentages of nonspawning, spawning, and spent females captured in Fishery Bay and in the lake during May, June, and July 1954–55 also give a basis for the estimation of the beginning, peak, and end of the spawning season of II-group and older shad.

The earliest samples containing spawning fish were captured in the first quarter of June on the spawning bar in Fishery Bay. The percentage of spawners caught here rose from 33.3 percent in that quarter to a high of 58.3 percent in the next quarter, then dropped to 45.0 percent in the third quarter and abruptly to 1.2 percent in the last quarter of June. Spawning shad were captured from the first quarter of June to the first quarter of July inclusive.

Although I lacked samples from the lake in the first quarter of June (the commercial fishermen of South Bass Island—the source of the lake-caught gizzard shad—did not fish during the last quarter of May and the first quarter of June) the Fishery Bay sample for that quarter and subsequent samples from the lake lead me to assume that spawning fish, though never numerous, were present here at that time also.

Spent fish were first observed in the first quarter

ABLE 20.—*State of ovaries of mature II-group and older gizzard shad captured in Fishery Bay and in Lake Erie in May, June, and July 1954–55*

[Given as percentages of fish in the categories "not spawning," "spawning," and "spent"]

Time of capture	Bay				Lake			
	Females	Not spawning	Spawning	Spent	Females	Not spawning	Spawning	Spent
ay:[1]	*Number*	*Percent*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Percent*
1–8	1	100.0	0.0	0.0	32	100.0	0.0	0.0
9–15	7	100.0	.0	.0	44	100.0	.0	.0
16–23	2	100.0	.0	.0	39	100.0	.0	.0
ne.								
1–8	51	64.7	33.3	2.0				
9–15	48	37.5	58.3	4.2	34	85.3	8.8	5.9
16–23	40	30.0	45.0	25.0	208	78.8	2.4	18.8
24–30	82	30.5	1.2	68.3	322	44.4	3.1	52.5
y:								
1–8	95	33.6	7.4	59.0	170	38.8	4.7	56.5
9–15	1	100.0	.0	.0	15	33.3	.0	66.7
16–23	2	100.0	.0	.0	14	.0	.0	100.0
24–31					5	.0	.0	100.0

[1] No females captured May 24–31.

of June in the Fishery Bay samples. Thereafter, all samples from both bay and lake showed increasing percentages of spent shad during June. In July, this trend persisted among the lake samples, but in the bay samples both spawning and spent fish were absent after the first quarter and only three nonspawning ones were captured. The available data indicate that the gizzard shad in western Lake Erie spawn during June and early July; the greatest percentage of them spawn in the second quarter of June.

Records of the average ovary weight as a percentage of the fish weight, for II-group and older female shad in 1954–55 (table 21), indicate that the ovary makes little increase in weight from the time the fish are spent until the following April. During that month, feeding increases (this is the first time in winter or spring during which recognizable food has been found in the shad's gut—table 24), but the fish weight decreases (table 9). Consequently, the combination of a little ovarian growth and loss of fish weight results in a rise in the ovary-weight/fish-weight ratio. This ratio is highest either in the last quarter of May, for which I have no samples, or the first quarter of June. In this period, more fish are just ready to spawn and fewer are spawning or are spent than at any subsequent period. Then, as more fish become partly or completely spent, the average ratio drops lower. The drop in June is steady, and in the last quarter of that month the ovary weight as a percentage of body weight is again at about the April level. I have no ovary weights for July, August, and September. However, since some shad are still spawning in July and follicular remains were yet to be absorbed, I suspect the low percentage of winter samples is not reached earlier than the last of July.

Table 21.—*The percentage of fish in the categories "not spawning", "spawning", and "spent", and the ovary weight as a percentage of the fish weight for II-group and older female gizzard shad, Lake Erie, 1954–55*

Period	Fish	Not spawning	Spawning	Spent	Ovary/fish weight
	Number	*Percent*	*Percent*	*Percent*	*Percent*
Oct	25	100.0	0.0	0.0	1.1
Nov	33	100.0	.0	.0	.9
Dec	20	100.0	.0	.0	1.5
Jan	1	100.0	.0	.0	1.1
Feb	4	100.0	.0	.0	1.8
March	1	100.0	.0	.0	1.5
Apr	102	100.0	.0	.0	2.4
May 1–8	33	100.0	.0	.0	3.8
May 9–15	49	100.0	.0	.0	4.2
May 16–23 [1]	41	100.0	.0	.0	4.3
June 1–8	51	64.7	33.3	2.0	9.9
June 9–15	81	58.0	37.0	5.0	8.5
June 16–23	113	47.8	16.8	35.4	5.3
June 24–30	102	16.7	.9	82.4	2.5

[1] No samples May 24–31.

The mature I-group gizzard shad spawn later than older fish. Ova of three fish captured during the 1954 spawning season (June 28, July 6, and July 8) were nearly ripe (fig. 10). These fish probably would have spawned in late July or early August, or else the ova would have been resorbed.

The eggs of the II-group fish which have been in the making for 1½ to 2 years—much longer than those of older fish—might be expected to be spawned earlier than those of older fish. Information on the older shad is too scanty, however, to permit study of this possibility.

The weight of the fish appeared to have no effect on the time of its spawning.

I tried two methods to determine the time of spawning within a 24-hour period. In one, a gill net was set on the previously mentioned spawning bar in the afternoon, lifted at midnight, reset immediately, lifted in the morning, reset again, and lifted in the afternoon. The numbers of shad of each sex were tabulated for each period. In the other method, concrete slabs with a surface area of 1 square foot were lowered to the bottom at the spawning site and examined for shad eggs three times daily, when the gill net was lifted.

Studies by the two procedures covered only 3 days, June 17–19, 1954; in 1955, the net method alone was employed (June 2–11). The gizzard shad spawned most actively in the evening and early night in 1954 and at night in 1955 (table 22); spawning was least in the daytime in both years. I have not seen shad spawning during the daytime, but have seen them milling actively, frequently breaking surface, when I lifted the net at midnight, especially in moonlight.

The individuals participating in the spawning change continually during the season, but a female does not deposit all her eggs during one nightly visit to the bar. Although the percentage of eggs remaining in the ovaries varies among individual fish throughout most of the spawning season, numerous partially spent fish with a substantial percentage of eggs still in the ovary are taken early in the season. Almost none carry large percentages of their eggs toward the close of the season. The state of development of the "nearly mature" ova and the free ones in the ovaries of

TABLE 22.—*Shad eggs and the spawning condition of gizzard shad collected during various periods of the day on a spawning site near Put-in-Bay, Ohio, in June 1954 and 1955*

Dates and period of day	Fish taken by gill nets			Eggs on concrete slabs [1]
	Males	Females		
		Not yet spawned	Partly spent	
June 17–19, 1954:	*Number*	*Number*	*Number*	*Number*
6:30 a.m.–7:30 p.m.	0	2	1	2
7:30 p.m.–12 p.m.	91	16	19	15
12 p.m.–6:30 a.m.	50	7	14	5
June 2–11, 1955:				
9 a.m.–4 p.m.	3	0	0	----------
4 p.m.–12 p.m.	48	4	7	----------
12 p.m.–9 a.m.	70	6	9	----------

[1] No observations in 1955.

spawning gizzard shad indicates possible periods of rest between spawnings.

The males captured on the spawning site during the period of most active spawning outnumbered the females three to one. This abundance of males may be attributed to one or more of the following: Their actual daily recruitment to the spawning site, their probable greater activity, or their possible longer stay on the site. I was unable to distinguish any degrees of "spentness" in the male.

Not having observed details of behavior of spawning gizzard shad, I can offer only the statements of others on spawning behavior. Langlois (1954) observed gizzard shad spawning on May 29, 1935, in North Reservoir at Akron, Ohio, near shore in 6 to 12 inches of water at a water temperature of 67° F. During oviposition, a female was flanked by a male on each side. No time of day was indicated. M. B. Trautman (personal communication) observed about 20 shad spawning in Buckeye Lake, Ohio, at 73° F. on May 23, 1939. The females, pursued by several males, swam rapidly toward a sloping stone wall, turned abruptly, and deposited their eggs. A. G. McQuate (personal communication) observed shad spawning in Sandusky Bay, Ohio, on May 24, 1954 (temperature 62.5° F.), along a stony shore near 12 m. (noon) in the shade of an overhanging tree. Female shad were pursued by several males. The fish frequently broke water.

My own failure to see gizzard shad spawning during the daytime at the spawning site in Fishery Bay can be attributed to their failure to spawn at that time. The small daytime catches in gill nets suggest that shad were extremely scarce at the site. I do not believe they avoided the gear, because the nets were treated with a copper preservative that rendered them greenish and, hence, less visible than untreated nets, and were set in aquatic vegetation which almost wholly obscured them. White bass, smallmouth bass, and rock bass, but very few gizzard shad, were caught in the day.

During the midnight lifts, however, when the moon shone brightly, I saw many fish swirling and breaking water. The moonlight was not bright enough for me to judge accurately the species or size. The gill nets caught many gizzard shad, however, during those nights and had many shad eggs adhering to the webbing. The only other fish caught at those times were a few carp.

Hatching and Early Development

The eggs of the gizzard shad are heavier than water and slowly sink after they are spawned. The egg capsules adhere to surfaces that they contact, such as submerged aquatic plants and stones. Experiments in the Ohio State Hatchery at Put-in-Bay indicated that the hatching time varies from about 36 hours to about a week, depending on the temperature. This finding agrees with Warner's [2] observations at Buckeye Lake, Ohio.

In a series of experimental hatchings over 2 seasons, I failed to keep the young alive beyond the 10th day after hatching. Mortality was low up to the 9th day and the fish appeared to be doing well; then suddenly on the 10th day only a few remained alive out of thousands. The remainder died before the day ended. Results were the same in running and aerated water and with various kinds of food, such as natural food from the lake and cultured protozoans.

The movements of the newly hatched gizzard shad were an upward swimming and a downward settling—in each direction the head was foremost. This behavior continued 3–4 days. The whole body moved sinuously with such rapidity that the individual movements could not be followed. At this time the pectoral fins were not yet used to any extent. On the fourth day the fry began to swim horizontally as well as upward and downward. Their mode of swimming at this age, observed (in a petri dish) under a dissecting microscope, was largely by the pectoral fins which "vibrated" seemingly with the rapidity of the wings of a bee in flight. The sinuous body movement was not abandoned, but the frequency had slowed enough that it could be followed easily.

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[2] Warner, E. N. 1940. Studies on the embryology and early life history of the gizzard shad, *Dorosoma cepedianum* LeSueur. Doctoral thesis, Ohio State University. (Unpublished.)

When food was added to the aquarium, the young shad darted to and fro as though pursuing some of the small particles. Although the digestive tract contained food during the fifth or sixth day, only green algae were recognized through the thin gut wall.

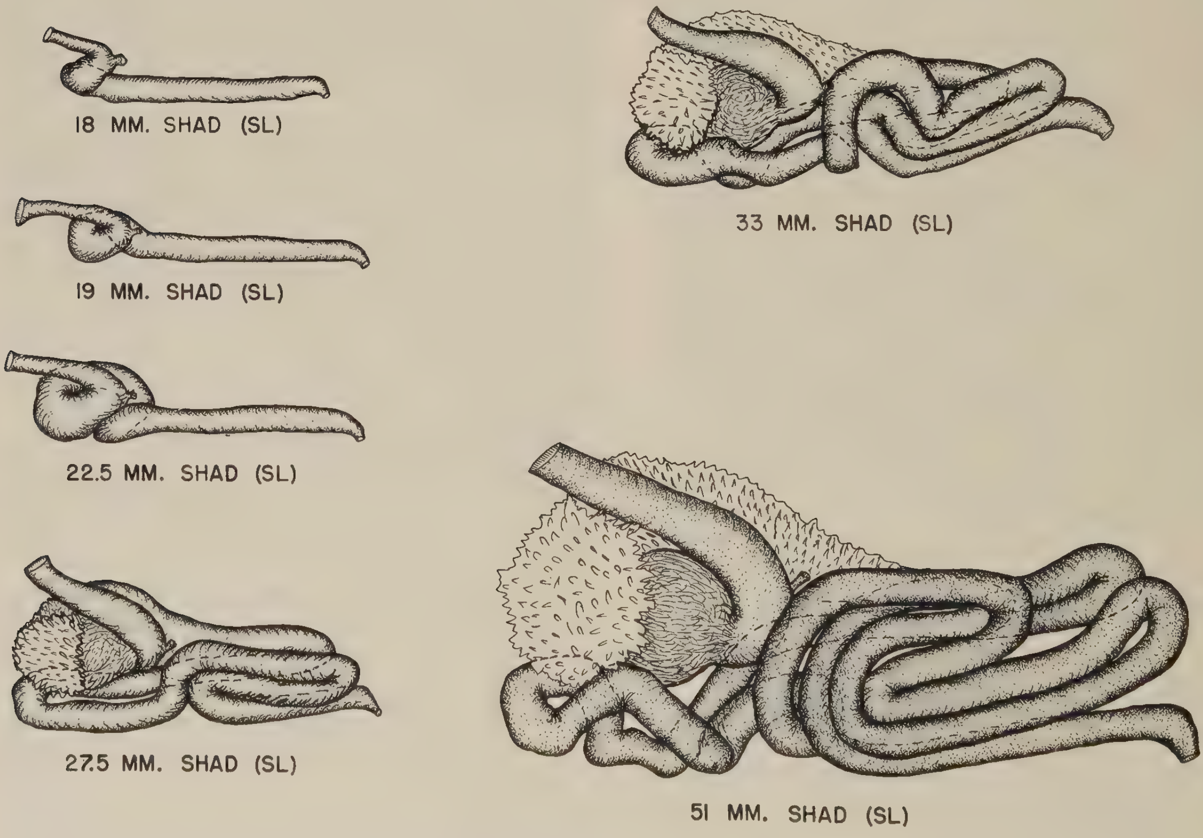
The young shad congregated on the lighted side of the aquarium. If all sides were lighted, they remained mostly near the source of the running water, facing into the current.

The first few days after hatching, the young gizzard shad subsists on its yolk. Increase in length of the 3.5 mm. newly hatched larva at this time results largely from the straightening of the cephalic flexures, after which the larva attains a length slightly greater than 5 mm. About the 5th day it begins to feed and by the 10th day has attained a length of slightly more than 6 mm. (in the laboratory). At this time it has a filiform shape, which it retains until it has reached a length of 20–30 mm. (fish from the lake—age unknown). Upon reaching this length, the shad begins to increase in depth. The filiform shape gives way to the slab-sided, deep-bodied adult form. Once this shape is acquired the form changes little and the shad begins to grow rapidly.

DIGESTIVE TRACT

Development of the Digestive Tract

The gut of a newly hatched gizzard shad is a tube which conforms to the body curvature. In the 10-day-old larva the gut is a simple, nearly straight tube. Among the older shad the gut of an 18-mm. fish (age unknown) had already developed two flexures (fig. 14). The 19-mm. shad had begun the third and fourth flexures, and the 22.5-mm. fry had already completed them. The portion



18 MM. SHAD (SL)

19 MM. SHAD (SL)

22.5 MM. SHAD (SL)

27.5 MM. SHAD (SL)

33 MM. SHAD (SL)

51 MM. SHAD (SL)

FIGURE 14.—Development of the shad gut (camera lucida drawings).

between the first and second flexures (later to become the gizzard) had enlarged. By the 27.5-mm. stage, the caeca had begun to develop from the duodenum (between the second and third flexures). As the gut continues to grow, the flexures move until they reach the limit of the abdominal cavity. Since the gut grows much faster in length than the abdominal cavity, secondary flexures are produced between the primary ones. Flexures provide landmarks by means of which one can determine relative rates of growth of the different portions of the gut. The caudal portion grows more rapidly and continues to grow over a longer period than any other section. No secondary flexures develop anterior to the third primary one.

Although the course of the gut of a young gizzard shad is complicated, it is relatively simple in comparison with that of the adult of, say, 250 mm., in which the convolutions are so numerous and complex that they defy tracing on a two-dimensional illustration. Indeed, the gut which amounted to one-half of the total length of the day-old fish becomes, in the adult, three times the length of the fish and is packed in an abdominal cavity, one-third of the fish's length.

Forbes (1914) stated that the larva of the gizzard shad has teeth. Although I have examined many young, from newly hatched to longer than 20 mm. (when the adult shape begins to take form), I have not observed teeth.

Digestive Tract in the Adult

The hundreds of long, thin gill rakers of the gizzard shad are admirably adapted for removing particulate matter from the water. This material, especially the filamentous algae and the small crustaceans, apparently is accumulated in the pharyngeal pockets, a paired muscular organ mentioned by Forbes (1888) and described by Lagler and Kraatz (1944). The thick muscular wall and the direct connection with the esophagus suggest that these pharyngeal pouches force their contents into the esophagus. The sphincter muscles in the forepart of the pneumatic duct prevent passage of food into the air bladder.

The muscular esophagus and the gizzard have been described by Wier and Churchill (1945). I can add only that the esophagus possesses longitudinal folds.

Numerous caeca arise in groups on the lateral surface of the duodenum. Each group has a common orifice through which the lumina of its caeca communicate with the lumen of the duodenum. These orifices are arranged in two parallel longitudinal rows. In a 200-mm. shad the lengths of the caeca range from about 5 mm. for those at the anterior end of the row to about 2 mm. at the posterior end. Counts were not made, but an individual appears to possess several hundred caeca. The caeca have internal longitudinal folds. Their lumina are so small that only the smaller unicellular organisms can enter. Although the caeca have the histological appearance of absorptive devices rather than secretory organs, it is only when the duodenum is turgid with food that any material is to be found here.

Wier and Churchill (1945) described a pancreas separate from the liver for the gizzard shad. I have been unable to identify one although I have searched for it repeatedly in many sizes of fish. These authors described the liver as composed of several lobes. I find that it has no definite form in the adult fish but rather seems to spread in close proximity to the gut. The liver invades intercaecal spaces as well as those between neighboring portions of the gut, and completely covers the anterior, dorsal, ventral, and left-lateral surfaces of the gizzard. It is a diffuse organ and intermixed, I believe, with the pancreas.

The small intestine possesses no villi, contrary to the statement of Forbes and Richardson (1908). It does contain four of the large, conspicuous, longitudinal folds described by Wier and Churchill (1945). Attached transversely between the folds and along the inner circumference of the gut are smaller folds or lamellae which have the free edge directed toward the center of the gut lumen (fig. 15). The free edge of each lamella is directed posteriorly at a slight angle. Although the columnar cell covering of these transverse lamellae is unquestionably absorptive and these structures greatly increase the absorptive surface of the gut, they may also function in the manner suggested to me by Milton B. Trautman. He suggested that during peristalsis the longitudinal ridges may lengthen and shorten, thereby causing the lamellae to move back and forth in venetian-blind fashion and, hence, to aid in forcing food along the tract.

This lamellar arrangement within the gut bears some resemblance to the situation described by

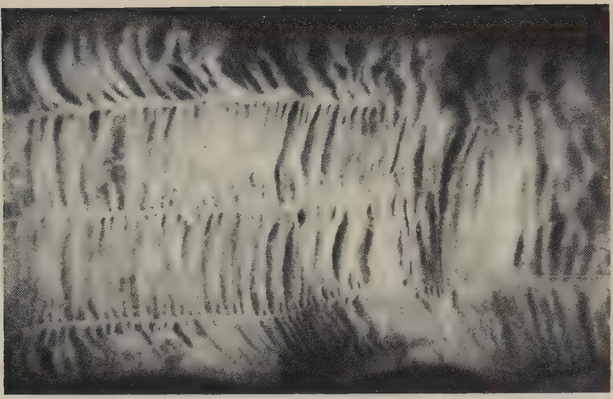


FIGURE 15.—Enlarged view of the small intestine of the gizzard shad showing three of the longitudinal folds with their transverse lamellae.

Kraatz (1924) for the gut of *Campostoma anomalum* in which somewhat similar folds assume a zigzag arrangement.

Transverse lamellae were present in a 22.5-mm. shad. Here they were attached circumferentially to the gut only—the longitudinal folds had not yet formed.

Longitudinal sections of the gut, because they cut across the lamellae, appear to be villous. This fact may account for the statement of Forbes and Richardson that the gut possesses villi.

Digestive Enzymes

Only a qualitative study was made of the digestive enzymes. Attempts to determine their quantity or potency did not yield dependably accurate results. The areas tested were: Pharyngeal pockets, esophagus, gizzard, duodenum (that forepart of the gut bearing the caeca), hepatopancreas, gall bladder, and the first, second, and third portions of the intestine. The materials were prepared in the usual manner and the extraction made with 50 percent glycerol.

Tests were made for the following enzymes: Pepsin, trypsin, amylase, lipase, maltase, sucrase, and rennin. In addition, I sought enzymes that would act on chitin and cellulose.

The enzyme giving the strongest reaction was amylase (table 23). It was present in all areas tested. The reactions for pepsin and trypsin were moderate, whereas the reaction for lipase was weak. I am at a loss to explain the significance of the positive test for rennin.

The presence of enzymes in the esophagus is not restricted to the gizzard shad. Sarbahi (1951) found amylase, maltase, and invertase in the esophagus of the goldfish, and Kenyon (1925) cited Kingsley as reporting gastric glands in the esophagus of the sturgeon.

FOOD AND FEEDING HABITS

The young gizzard shad begins to feed about 4 or 5 days after hatching. The earliest food is probably Protozoa and unicellular algae. When the shad has attained a length of about 20 mm., it feeds on the smaller of the zooplankters and takes practically no phytoplankton. By the time it is 30 mm. long it has assumed the adult shape, and its gizzard is fairly well developed. The fish now begins to feed more and more on phytoplankton.

Three opinions have been offered in the literature regarding the nature of the food of adult gizzard shad. Some believe they eat predominately mud; others insist that they feed almost wholly on

TABLE 23.—*Digestive enzymes found in the gizzard shad*

[If no value is given, a test was not made. The numerical ratings are: 0, negative; 1, not definite; 2, perceptible; 3, small; 4, considerable; 5, strong]

Enzyme	Area tested								
	Pharyngeal pockets	Esophagus	Gizzard	Duodenum	Intestine			Hepato-pancreas	Gall bladder
					1st part	2d part	3d part		
Pepsin	0	3	4	3	0	0	0	2	0
Trypsin	0		0	4				3	2
Amylase	3	3	3	4	4	4	3	5	4
Lipase	0	0	1	2	0	0	0	3	2
Maltase	0	0	0	1	0	0	0	1	1
Sucrase	0	0	0	2	0	0	0	0	0
Rennin	0	0	1	3				3	0
"Chitinase"	0	0	0	0	0	0	0	0	0
"Cellulase"	0	0	0	0	0	0	0	0	0

TABLE 24.—*Monthly record of occurrence of various items in stomach contents of gizzard shad in 1952–55*

Month	Material in digestive tract											
	Debris	Sand	Diatoms	Dinoflagellates	Blue-green algae	Green algae	Protozoans	Rotifers	Ostracods	Copepods	Cladocerans	Insect larvae
Jan	X	--	--	--	--	--	--	--	--	--	--	--
Feb	X	--	--	--	--	--	--	--	--	--	--	--
Mar	X	--	--	--	--	--	--	--	--	--	--	--
Apr	*X	X	X	--	--	X	--	X	--	--	--	--
May	*X	X	X	--	--	X	--	--	--	X	--	--
June	*X	*X	*X	--	--	*X	X	*X	--	*X	*X	X
July	X	*X	*X	X	*X	*X	X	*X	X	*X	*X	X
Aug	X	*X	*X	X	*X	*X	X	*X	X	*X	*X	X
Sept	X	X	X	--	X	*X	--	X	--	X	X	--
Oct	X	X	*X	--	--	*X	--	X	--	--	X	X
Nov	X	--	*X	--	--	*X	--	X	--	X	X	--
Dec	X	--	--	--	--	--	--	--	--	--	--	--

*Indicates the more plentiful items.

phytoplankton; still others maintain that they subsist mostly on zooplankton. All agree, however, that they are "filter-feeders," and this feature alone, I believe, best describes their feeding habits. They filter the water of whatever particulate matter it contains. Shad captured in open waters contained mostly free-floating phytoplankton; those captured among the attached plants, such as *Cladophora*, *Myriophyllum*, and *Ceratophyllum*, ingested Cladocera, Copepoda, Rotifera, and small aquatic insect larvae; those captured in very turbid waters were filled largely with mud. That they do, however, add to their diet from the bottom debris is evidenced by the presence in the gizzard of sand particles of diameters in excess of 0.25 mm. This size of sand is not held in suspension even when the water is highly turbid. Although the bottom is available to the shad at all times, I have not found sand in shad gizzards from December through March. Food particles could not be identified during this period. The taking of sand when food is plentiful suggests its use as an aid in grinding by the gizzard—or it may have been taken accidentally along with food.

The appearance of the food differs in the three distinct regions of the alimentary apparatus—the pharyngeal pockets, the gizzard, and the intestine (especially the forepart which bears caeca and which is often swollen with ingested material). When reference is made to food in the gizzard shad without regard to a definite region of the digestive tract, I use the term "stomach contents."

The pharyngeal pockets, suggested by Lagler and Kraatz (1944) to be accessory to the digestive system, have, to my knowledge, not been thoroughly examined in studies of food of gizzard shad. The pouches frequently are empty, but when food is plentiful and the fish's gut is full of food (especially zooplankton), the pharyngeal pockets contain as much food as the gizzard. The contents of these pockets appear straw-colored and consist mostly of Cladocera and Copepoda along with strands of filamentous algae. Here are found the larger items of the shad's diet, and they are, as yet, not broken apart. The zooplankters still have their full complement of appendages and the filamentous algae are in strands.

The gizzard is frequently empty, and only rarely is it turgid with food. The composition of food in the gizzard is similar to that of the pharyngeal pockets. The zooplankters, however, are more or less dismembered, and the strands of filamentous algae are short. The gizzard contains, in addition, many unicellular algae, rotifers, and some sand along with plant and animal debris.

The intestine usually contains food, although the amount is scanty in winter. Material from the intestine is fragmented and mostly unrecognizable—it has the appearance of bottom debris or mud, especially on gross inspection.

I have found no compact matter exceeding a diameter of 3 mm. in the stomach contents of gizzard shad, except Tendipedidae and small *Leptodora* during certain seasons. Nor have I found in them bits of attached aquatic plants, except after severe storms when small fragments were presumably torn loose and were recovered by the filtering apparatus.

The stomach contents of adult gizzard shad exhibited no appreciable differences among individual shad of a group collected in a locality at the same time. Evidence was lacking for any selection of food within the size range of material they swallow. There were, however, local and seasonal differences related, undoubtedly, to the abundance of the various forms in different places and at different times. As a result of these observations, examination of stomachs of individual fish was soon discontinued and the stomach contents of several fish of a collection were combined.

The feeding habits of gizzard shad were well summarized by Tiffany (1920) who indicated them to be a living tow net. No attempt was made in the present study either to obtain the percentage of each item ingested or to enumerate every organism eaten by the shad at one time or another. In table 24 are listed only major groups of materials found in shad during various months. The table does not identify the months in which the gut contained the most food; in general, the quantity was more plentiful when the diet consisted of a great variety of food in June through November.

Velasquez (1939) cultured algae taken from various parts of the shad gut. As a result either of rapid transit through the gut, or absence of certain enzymes, some algae or certain algae apparently are not utilized as food.

SUMMARY

This study of the life history of the gizzard shad was based on records of the length, weight, and age of almost 24,000 specimens taken in western Lake Erie in 1952–55. Approximate numbers of fish employed in other phases of the study were: calculation of growth from scale measurements, 700; seasonal fluctuations of gonad weight, 700; sex ratio and maturity, almost all fish over 120 mm. long; feeding habits, 200; seasonal development of ovaries, 150; and fecundity, 13.

The fish were captured by means of dip nets, "Common Sense" seines, bag seines, push seine, gill nets of various mesh sizes, regulation commercial trap nets, and by electric shock, dynamite, and rotenone. Fish older than the O-group were captured mostly by the gill nets and trap nets. Most fish were captured within one-half of a mile of the Bass Islands.

The scales of the gizzard shad are described briefly. Two types of annuli are present—a narrow clear-cut line of demarcation and a wider, more evident one. The first annulus is always of the former variety; the second and succeeding ones (with few exceptions) are of the latter variety. The wider, obvious annulus may be a combination of an annulus and a spawning check, while the narrow variety is strictly an annulus.

The time of annulus formation varied with age and sex. Some of the I-group shad began to form the new annulus in May, and all had it by the end of the first quarter of June. Annulus formation of older shad began in June and was completed by mid-July. Females seem to have formed their new annulus about a week earlier than the males. Spawning of these older females occurred while annulus formation was in progress—some fish spawned before the appearance of the new annulus—some after its appearance. Although prespawning development of the gonads was thought to affect the physical appearance of the annulus, the spawning act appeared to have no effect on the time of its appearance. Evidence was given that the annulus is a true year mark.

The body-scale relation was a straight line with an intercept of 22.1 mm. on the axis of standard length.

Calculated lengths showed good agreement with empirical lengths of shad captured between the first of the year and the time of annulus formation—except for the I group. The greater average length of I-group fish at capture can be attributed to gear selectivity.

Sampling problems made the determination of age composition difficult. The young gizzard shad were found in shallow water, the older in deeper water, and the very oldest were captured only during the spawning season. Shad captured in the open lake during fall probably gave the best available estimate of the relative strength of younger age groups. Those captured during the spawning season were most nearly representative of the age composition among the older shad. On these assumptions the following survival from an original 100,000 I-group fish were computed: II-group, 5,534; III-group, 435; IV-group, 63; V-group, 11; and VI-group, 6.

The 1952 year class was one of more than usual abundance. In 1953, as I-group they constituted

85 percent of the fish caught; in 1954, 71 percent as II-group; and in 1955, 11 percent as III-group.

Males made up 45.6 to 49.7 percent of the fish in the four younger age groups (O–III). They were less abundant (36.6 percent) in the age groups IV–VI combined. During the spawning season the percentage of males on the inshore spawning site was greater than normal but that in the open lake was less.

The length-weight relation of gizzard shad varies from year to year, from season to season within the year, according to sex during the spawning season, and among the females according to the state of the ovaries during the spawning season.

Equations were derived for length-weight data and from them was obtained the general length-weight equation, $\log W = -4.81765 + 3.07053 \log L$, in which W is the weight in grams and L the standard length in mm. Gizzard shad from Lake Erie were heavier than those reported from Illinois and Missouri.

Fish of the same length had the greatest weight in August–October. Males were lightest in June; females in May. The spawning-season female was heavier than the male; this difference in weight was not traceable to the gonadal development in the female, but may result from the greater activity of the male at this period. Among the females in the spawning season, those which would not spawn during the current season were the heaviest, those approaching spawning were next, and spent fish were the lightest. The percentage loss in weight during spawning averaged 10.7.

Annual differences in shad weight from relatively heaviest to lightest ran: 1952, 1954, 1955, 1953.

Most of the growth in length for the O-group (which hatched in June) occurred in July–September; for the I-group during June–August; and for the II-group during July–September. Gizzard shad of the II-group and older commence their rapid growth in length about a month later than the I-group fish. Shad lengths remain practically stationary from November until the time of annulus formation.

Males and females had almost the same length at the end of the first year (140 mm.) but after about June of the second year of life the females were consistently longer than males of corresponding ages. The sizes of males and females at the start of different growing seasons were: third, males, 273 mm. and females, 285 mm.; fourth, males, 313 mm. and females, 335 mm.; fifth, males, 343 mm. and females, 364 mm.; sixth, males, 349 mm. and females, 386 mm.

The seasonal growth in weight resembles that of the growth in length except that weight decreases during winter while length remains nearly constant. This loss of weight begins about the start of the year and continues until about May.

Differences among the lengths of individuals of an age group at the end of a calendar year tend to be reduced by later compensatory growth. At the end of succeeding years those fish that were the longest of their year class maintain a length advantage, but this advantage decreases.

The stage of egg development varied from fish to fish throughout most of the year, but with the approach of the spawning season, the retarded shad increased their pace of development while the advanced ones slowed down so that the condition of the ovaries became much more nearly uniform.

A brief description is given of the testis and of various stages of the ovary. The developing egg and the seasonal changes in the saccular ovary also are described.

Not all mature eggs are expelled at the same time. Eggs which are not mature are held over for next year, and those which develop to the spawning stage too late to be expelled are resorbed.

Only rarely were I-group female shad ripe. Most of them (an estimated 80 percent) spawn for the first time as II-group fish. The age of sexual maturity could not be determined for the male; males examined in January had motile sperm—even the new I group. The number of II-group males on the spawning site suggests that most mature as the II-group—the few I-group individuals present may be termed precocious.

A spawning site in the vicinity of Fishery Bay, South Bass Island, was a sandy, rocky bar covered with 2–4 feet of water. Gizzard shad were captured here only during the spawning season—almost all during the evening and night. Spawning was limited in the open lake. The females that are ready to spawn migrate to inshore spawning sites. After spawning, they return to the deeper water. Males also migrate to the spawning sites where they are two or three times as numerous as the females. The representation of the sexes was nearly equal in the open lake at this time. Spawning was most active in the evening and early night in 1954 and in the night in 1955.

Spawning occurred from the first quarter of June through the first quarter of July; peak spawning was in the second quarter of June. The precociously mature I-group fish spawn in late July or later.

The II-group shad produce the greatest number of eggs—about 379,000. In decreasing order are: III-group, 345,000; IV-group, 309,000; VI-group, 215,000; and the precocious fishes of the I-group, 59,000.

On the basis of eggs per gram of fish, relative fecundity triples from age group I to II and then declines to age group VI, which has about the same value as the I group.

The eggs of the shad hatch in 1½ to 7 days, depending on the temperature. The movements of young fry are described.

The gut of a small larva is a nearly straight tube. Sometime after the 10th day the gut begins to fold. The convolutions become more and more complex with increasing size. The gizzard becomes evident in the 22.5-mm. stage. The liver is a diffuse organ, apparently mixed with the pancreas; no pancreas was found.

The intestine lacks villi but has longitudinal folds and transverse lamellae which increase the absorptive surface and may help move the food along during peristalsis.

The presence of sand in the gut when ingested food is plentiful and its absence in winter, when the gut is empty, suggest that it may be taken as an aid in grinding the food in the gizzard.

Food was frequently present in the pharyngeal pockets of large gizzard shad whose gizzard and intestine were packed with food. The presence here of long strands of filamentous algae, and Cladocera and Copepoda with their full complement of appendages, repudiates statements that they are regurgitated into the pockets. In the gizzard, these items were always in some stage of dismemberment.

Tests were positive for the following digestive enzymes: pepsin, trypsin, amylase, lipase, and rennin. Amylase was found in all areas of the tract.

The earliest food of gizzard shad appears to be Protozoa. At a length of about 20 mm., shad feed almost wholly on the smaller of the zooplankters. After the 30-mm. stage, the digestive tract contains greater and greater percentages of phytoplankters. "Filter feeders" best describes the habits of adults. Zooplankters or phytoplankters may predominate in the gut according to their abundance in the water in which the fish are feeding. By the time the food reaches the intestine it has been macerated and partially digested so that it resembles mud. This fact may explain the frequent statement that shad eat mud.

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BIOACCUMULATION OF RADIOACTIVE GOLD USED AS A SEDIMENT TRACER IN THE ESTUARINE ENVIRONMENT[1]

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ABSTRACT

The accumulation of radioactive gold by selected members of a marine animal community and sediment material was followed under laboratory and field conditions. In the laboratory an aqueous solution of radioactive gold was placed directly in the gut of blue crabs, toadfish, and croakers. There was little transfer of the isotope to various tissues in these organisms. A group of toadfish which were fed radioactive gold in an aqueous solution retained more of the isotope than did a group which were fed the same amount of radioactivity sorbed onto clay particles. Also, crabs, fish, clams, and samples of bentonite clay were maintained for 25 days in 1,000 liters of cotton-filtered sea water containing radioactive gold. Crabs accumulated the most radioactivity followed, in descending order, by clams, clay, and fish. A field experiment was conducted in cooperation with the U.S. Army Corps of Engineers in the Cape Fear River, N.C. Caged and indigenous free-swimming organisms were exposed to sediment-sorbed radioactive gold used as a sediment tracer by the Corps. Oysters, crabs, and fish maintained in cages in the experimental area were sampled periodically. The maximum level of radioactive gold in the caged organisms (70.9 millimicrocuries per gram wet weight tissue) was detected in oysters 17 hours after the isotope was released. Indigenous organisms collected 41 hours after the radioactivity was released contained no detectable radioactive gold.

The uncontrolled release of radioactivity into estuarine waters could so contaminate marine organisms that they would be unsafe for use as food by man. However, with the use of basic data from laboratory experiments to evaluate the quantity and rates of release of radioactive materials, and with sensitive instruments to measure the resulting levels of radioactivity, radioisotopes can be released into the natural environment without adversely affecting seafood organisms. Also, when released in this manner, radioisotopes can safely be used *in situ* to investigate many ecological problems.

A study was made to determine the bioaccumulation of sediment-sorbed radioactive gold released into the Cape Fear River. This study was carried out with investigators of the U.S. Army Corps of Engineers, who used this isotope to trace sediment movement in the river. Prior to this investigation, radioactive gold had been used successfully as a sediment tracer by the Corps of Engineers in several bays and harbor systems in the United States.

Determinations of gold in marine organisms have been reported by Noddack (1939), Vinogradov (1944), and more recently by Fukai (1962). Equilibrium values for the distribution of gold between sea water and organisms have been calculated by Krone (1959) using the data of both Noddack and Vinogradov. The capacity of marine organisms to accumulate radioactive gold from contaminated sea water or from contaminated food organisms has not been determined.

Since marine organisms could be exposed to radioactive gold used in sediment tracer experiments, an evaluation of the accumulation of this isotope by several marine organisms was made by (1) conducting laboratory experiments to deter-

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[1] The work upon which this report is based was done under the cooperative agreement between the Fish and Wildlife Service, U.S. Department of the Interior and the U.S. Atomic Energy Commission.

mine the behavior of gold in sea water, and the translocation of this element in several animals; (2) observing the transfer of radioactive gold from sea water to a community maintained in a large salt-water tank; and (3) measuring the accumulation of the isotope in animals and sediments in the natural environment.

PRELIMINARY LABORATORY EXPERIMENTS

The behavior of radioactive gold in sea water, its affinity for sediments, and its assimilation by individual organisms were studied prior to following the movement of radioactive gold through a community of organisms. Characteristics of radioactive gold in sea water and the effect of salinity on the sediment-sorption of this isotope were observed. Bentonite clay composed of montmorillonite clay minerals was used in the sediment-sorption experiments because of the natural occurrence of these minerals in marine sediments and because of their reported sorptive properties (Grim, 1953). Experiments on the assimilation of radioactive gold by individual animals were conducted in sea water ranging in salinity from 28 to 32 °/₀₀ and having a temperature range of 27.0° to 30.2° C. These animals included blue crabs, *Callinectes sapidus;* oyster toadfish, *Opsanus tau;* and Atlantic croakers, *Micropogon undulatus;* all collected near Beaufort, N.C.

Gold 199 was selected in preference to gold 198 because of its longer half-life (3.1 days compared with 2.7 days) and its availability in the carrier-free form (2.09×10^5 curies (c.)/gram). The gold 199 in the form of auric chloride was supplied from Oak Ridge, Tenn.

The radioactivity content of sediment, water, and animals in these preliminary experiments was measured with a scintillation detector large enough to contain live animals (4¼ inches diameter by 9 inches long) and a single-channel gamma spectrometer. Measurements were corrected for decay, geometry, and background.

BEHAVIOR OF RADIOACTIVE GOLD IN SEA WATER

The behavior of tracer amounts of radioactive gold in aqueous solutions was investigated by Schweitzer and Bishop (1953). These investigators have shown by filtration and centrifugation that gold (in concentrations less than 10^{-8} M) appears to behave as a radiocolloid in certain aqueous solutions ranging in pH from 2 to 12. Schweitzer and Jackson (1952) also discussed the use of cation exchangers in the identification of radiocolloids. The uptake of a cationic tracer by an exchanger should decrease with an increase in the cationic concentration of the solution. If the tracer is a radiocolloid, however, the uptake increases as the cationic concentration increases. This is attributed to the effects of the cations acting as a coagulant and the exchanger acting as an absorbent.

Several experiments were conducted in this study to determine, qualitatively, the behavior of radioactive gold in sea water. A water sample was prepared by adding 200 microcuries (μc.) of gold 199 (4.9×10^{-11} M) to 1 liter of Millipore-filtered sea water of 30 °/₀₀ salinity and a pH of 8.2. The temperature of the water was maintained at 25°±2° C. during the experiment. Centrifugation of 500 ml. of this sample at 3,000 r.p.m. for 15 minutes forced 58 percent of the radioactivity to the bottom of the tube indicating that gold particles had been formed. When 500 ml. of the initial sample were passed through a Millipore filter of 45 millimicrons (mμ) pore diameter, 100 percent of the radioactivity was removed. Even though some of the gold could have been retained as a result of pores being clogged by large molecules, the gold in sea water appeared to be particulate, rather than ionic.

Further indications of the properties of radioactive gold in sea water were obtained by observing the sorption of gold onto clay. Equal amounts (200 μc.) of gold 199 were placed in four tanks, each containing 1 liter of millipore-filtered water and 1 g. of clay. The first tank contained distilled water; the second, water having a salinity of 8°/₀₀; the third, 24°/₀₀; and the fourth, 34°/₀₀. The waters having salinities of 8°/₀₀ and 24°/₀₀ were prepared by adding appropriate amounts of distilled water to sea water having a salinity of 34°/₀₀. The water in the tanks was agitated for 15 minutes and allowed to stand for 24 hours. The clay slurry was withdrawn from each tank, centrifuged, and the water decanted. The clay was then dried and the amount of radioactive gold measured.

The uptake of gold 199 on clay increased as the salinity increased (fig. 1). There are at least two possible explanations for this sorption phe-

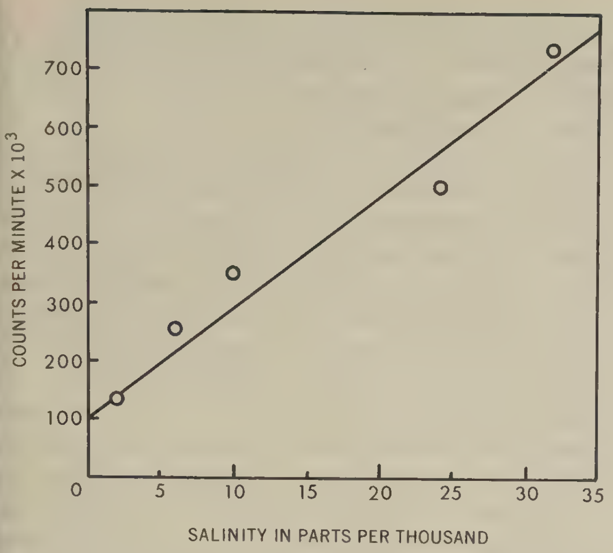


Figure 1.—Sorption of gold 199 by montmorillonite clay from sea water with increasing salinity.

nomenon: (1) An increase in salinity caused the clay to clump, and radioactive gold was trapped within the clumps; and (2) The increase in salinity caused the gold particles to coagulate and to sorb more readily onto the clay. If the latter explanation is accepted as correct, it would appear that radioactive gold was colloidal in this sample of sea water.

DISTRIBUTION OF RADIOACTIVE GOLD IN BLUE CRABS

Edible portions of an organism such as a blue crab can be relatively free from radioactivity even though the total radioactivity content of the organism is high. This is possible when the activity is isolated in the stomach or associated with the highly sorptive carapace and other external sites. That this does occur was shown by determining the distribution of ingested radioactive gold in the blue crab. Twelve crabs with an average weight of 152 g. were made radioactive by pipetting 75.7 μc. (50 microliters) of gold 199 directly into the cardiac stomach of each crab. They were then placed in flowing sea water. At intervals of 3, 4, and 5 days after dosing, three crabs were killed, dissected, and measured for contained activity.

Radioactivity content of tissues at 4 days indicated that only a small portion of the gold 199 was assimilated from the stomach (table 1). In view of the short half-life of the isotope, more than tracer amounts of radioactive gold would need to be ingested rapidly in order to build up concentrations in edible tissues.

DISTRIBUTION OF RADIOACTIVE GOLD IN TOADFISH

Bottom feeders, such as the oyster toadfish, could become radioactive by taking in sediments with loosely bound sorbed activity. If the radioactivity were tightly bound to the sediment particles, however, the sediment-sorption phenomenon would reduce the possibility of animal contamination by retaining and confining the radioactivity.

Table 1.—*Radioactivity content of crab tissue 4 days after an oral dose of 75.7 μc. of gold 199*

Tissue	Activity	Dose in entire tissue
	μc./g.	*Percent*
Digestive gland	9.3×10^{-1}	12
Stomach—gut	8.4×10^{-1}	3
Gonad	1.6×10^{-1}	.8
Gills	5.3×10^{-2}	.7
Muscle	2.5×10^{-2}	.6
Carapace	3.8×10^{-3}	.08
Blood	1.7×10^{-3}	.04
Total		17

To test the capacity of fish to "strip" radioactive material from sediments, five male toadfish, average weight 325 g., were each force-fed 75.7 μc. of radioactive gold dispersed in 2 ml. of sea water. Five other males of similar size were fed the same amount of radioactivity sorbed onto 25 mg. of montmorillonite clay suspended in 2 ml. of sea water. The sea water used in both instances had a salinity of 30°/₀₀ and a pH of 8.1. After the fish had been fed the isotope, they were placed in flowing sea water. Forty-eight hours later, the fish were killed and dissected, and the amount of radioactive gold in various tissues was measured.

A comparison of the activity of tissues from both groups of fish shows that most of the gold remained sorbed onto the clay as it passed through the digestive system of the fish (table 2). The fish fed the isotope in sea water retained more activity than those fed the isotope sorbed onto clay.

DISTRIBUTION OF RADIOACTIVE GOLD IN CROAKERS

The gastro-intestinal absorption and distribution of gold 199 in the tissues of the croaker were determined after 75.7 μc. of the isotope were

Table 2.—*Radioactivity content of toadfish tissues following oral doses of gold 199*

Tissue	Gold administered in solution	Gold administered sorbed onto sediment
	μc./g.	*μc./g.*
Stomach	3.6×10^{-1}	6×10^{-3}
Liver	1.5×10^{-1}	8×10^{-4}
Gut	1.1×10^{-1}	5×10^{-2}
Gill	4.3×10^{-2}	2×10^{-4}
Kidney	4.0×10^{-3}	1×10^{-3}
Blood	4.0×10^{-3}	5×10^{-4}

pipetted into the stomachs of six fish. The fish were then placed in flowing sea water. Three were killed, dissected, and tissues were measured for radioactive gold content after 78 hours and three after 148 hours.

Less than 1 percent of the dose was assimilated by the tissue, about 99 percent having been eliminated within 78 hours (table 3). Of the relatively small amount assimilated, kidney and gills had the highest concentrations of gold 199 per unit weight. After 148 hours the gills and spleen had the highest concentrations. The increase in gold 199 content in some of the tissues during the period from 78 to 148 hours is probably the result of continued assimilation from the digestive tract and translocation of gold 199 from other tissues.

Table 3.—*Distribution of radioactive gold in croaker tissue*

Tissue	Dose	
	78 hours	148 hours
	Percent	*Percent*
Kidney	0.038	0.01
Gills	.035	.056
Skin, scales	.017	.009
Liver	.006	.02
Muscle	.003	.03
Heart	.002	.0008
Spleen	.001	.042
Gonad	----------	.001

EXPERIMENTAL ENVIRONMENT STUDY

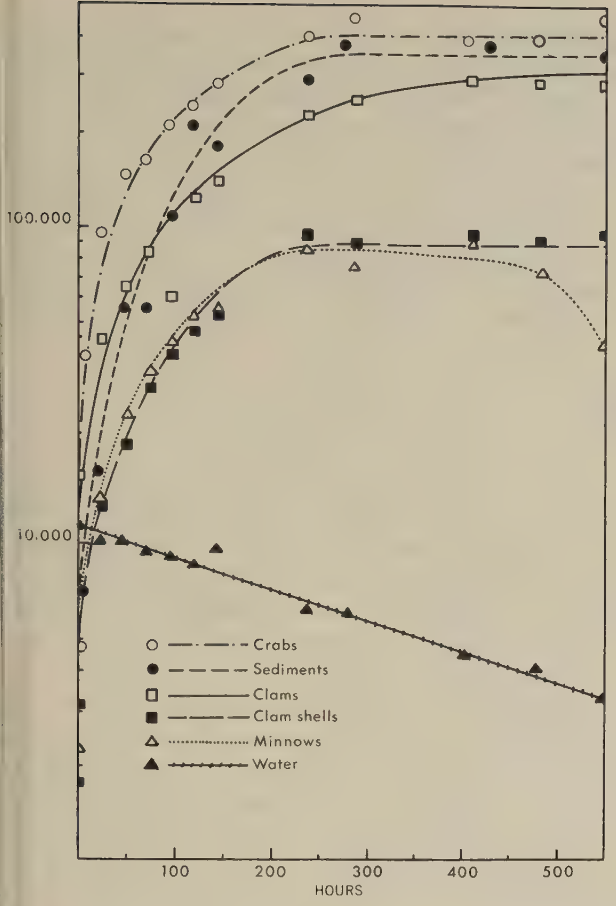
Since the planned application of radioactive gold in the Cape Fear River would expose the community of indigenous organisms further laboratory studies were conducted with a marine community maintained in a large tank. Data obtained from tank experiments involving relatively large volumes of sea water (1,000 l.) and a community of organisms have advantages over data for individual species held in smaller volumes of water. Increasing the volume of water enlarges the experimental environment, and chronic as well as acute contamination can be observed since observations can be made over longer periods of time because of the improved physiological condition of the organism.

An experimental environment was established to follow the movement of radioactive gold in a marine community. The community, which consisted of clams and clam shells, *Mercenaria mercenaria*; blue crabs; and sheepshead minnow, *Cyprinodon variegatus*; as well as sediment samples of clay, was installed in a large (172 by 117 by 61 cm.) fiberglass tank containing 1,000 l. of cotton-filtered sea water (table 4). Ten clams were placed directly on the bottom of the tank, and 10 in the sediment. Enough gold 199, as $AuCl_3$, was added to the water to give a concentration of 0.0142 μc/ml. After the gold was added, the pH of the water was 8.1. Throughout the experiment the water temperature was maintained at 21°± 3° C. and the salinity at 32 ± 0.10‰, the latter by adding distilled water when necessary to compensate for evaporation. A plastic impeller pump circulated the water continuously.

Clay sediment introduced into the tank was first placed in glass bowls (3 cm. deep by 12.7 cm. in diameter) after being thoroughly wetted as follows: 6 kg. of clay were suspended in 10 liters of sea water for 48 hours, and the excess water was decanted from the clay, leaving it with a pastelike consistency. In each bowl, 200 g. of the wet clay (125 g. dry weight) were placed forming a smooth substrate that was not disturbed by water circulation.

The radioactivity content of whole animals and sediment was measured periodically, with the organisms afterward being returned to the tank. Oysters, clams, and crabs were prepared for radioactivity analysis by wrapping them in a thin transparent plastic sheet. Fish were placed in dark glass jars containing nonradioactive sea water and counted for 3 minutes. Sediments were removed from the tank with a small diameter (2.5 cm.) core sampler and were not returned to the tank. This procedure of measuring the activity in a whole animal eliminated the need for killing it, and the number of individuals was not reduced with sampling. Also, uptake could be followed on the same individual throughout the experiment.

Appropriate corrections were made for decay, geometry, and background on all radioactivity measurements unless otherwise stated.



IGURE 2.—Movement of gold 199 in an experimental marine environment.

TABLE 4.—*Composition of experimental environment showing distribution of gold 199, 600 hours after introduction of the isotope*

Component	Individuals	Total wet weight	Gold 199 content after 600 hours
	Number	*G.*	*μc.*
Water		1.0 x 10^6	4,600
Sediment		1,000	330
Crabs	5	620	340
Clams	20	2,800	1,100
Clam shells	10	130	10
Fish	10	46	230
Total uptake by components			6,610
Loss unaccounted for			7,590

Components of the community rapidly accu- ulated radioactive gold and reached an apparent eady state after 225 hours (fig. 2). There was ot a direct relation between the accumulation of e radioactive gold by the components and the ss of the isotope from the water. Even though e radioactive content of the organisms and diments did not increase after 225 hours, the dioactivity content of the water continued to ecrease. This decrease was attributed to sorpon of the radioactivity to exposed surfaces in the nk (a total area of 29,784 cm.²) and to accu- ulation by patches of bacterial film that appeared the sides of the tank after the experiment had en in progress about 120 hours. Although it as not possible to measure the total amount of m present, 1 g. of this material contained 57 . of radioactive gold after 600 hours. The stribution of the radioactive gold in the community at the end of the experiment is shown in table 4.

Crabs accumulated more radioactive gold than the other organisms in the experiment. As an estuarine species, blue crabs are a part of a marine community that appears most likely to be exposed to radioactive material in any appreciable concentration. As bottom-dwelling, omnivorous predators and scavengers, blue crabs are, at one time or another, in contact with almost all of the abiotic components of their environment. The carapace and gills offer many surface sites for sorption of materials from the environment. Gill area alone of a blue crab has been estimated to be about 275,000 mm.² (Gray, 1957).

Although sediments often are not included in the food web of marine organisms, many organisms can utilize materials sorbed onto sediments as a source of nourishment. Thus, it is necessary to observe accumulation of gold by sediments as well

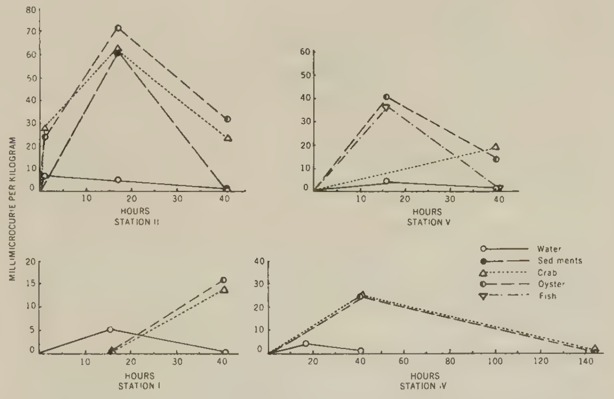


FIGURE 3.—Sorption of gold 199 by sediment in an experimental environment. Curve *A* is activity corrected for decay, curve *B* is observed activity.

as accumulation by the biota. In the present experiment, an increase in sediment activity up to the 250th hour occurred (figs. 2 and 3). From this time until the experiment ended, the activity was maintained with no significant increase or loss; it appears that the sediments were saturated with gold at 250 hours (curve A, fig. 3). The actual activity of the sediments, uncorrected for decay, is shown in curve B of figure 3. The latter values would be of more importance to the health physicists, as they show the actual amount of activity present in the sediments. If the gold were released into sea water in a restricted area where dispersion was minimal, these results indicate that natural decay would exceed uptake after about 150 hours with a resulting decrease in sediment activity.

Live clams accumulated more radioactivity than did the separated clam shells. Since clams feed by filtering suspended matter from large volumes of water passing over their gills, they are susceptible to contamination from particulate radioactive materials released into the estuarine environment. As bottom dwellers, restricted in their movements, they are in contact with sediments and associated radionuclides. A comparison of the mean radioactivity content of 10 clams to 10 separated clam shells on a unit weight basis by a standard *t* test at the .05 level showed that live clams were significantly more radioactive. The higher concentration of the isotope in the live animals was attributed to the movement of water through the animals. This movement would expose internal tissues as well as shell surfaces to contaminated water.

The clams placed on top of the sediment at the beginning of the experiment accumulated much less radioactive gold than those placed in areas without sediment. As the experiment progressed, the clams burrowed into the sediments, leaving only a portion of their shells exposed. The burrowing clams contained 38 percent less activity than those that remained on the bottom surface of the tank—an indication that a large portion of the gold accumulated by clams was due to sorption of the shell.

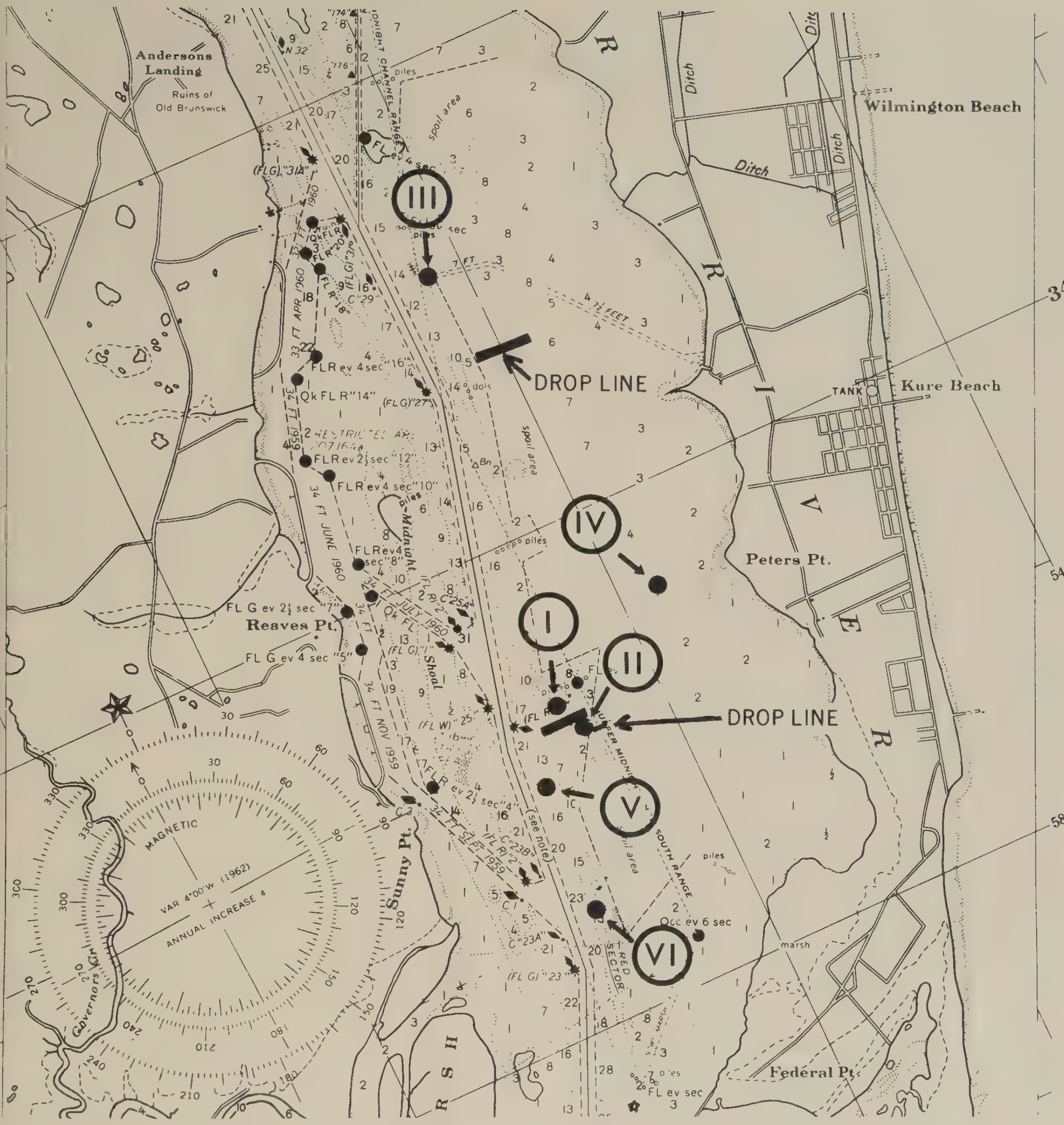
Fish accumulate radioactive materials by adsorption, absorption, or by ingestion. In nature, these three modes of uptake can occur simultaneously, singly, or in various combinations, depending upon the physical state of the isotope in the water, the food habits of the fish, and the length of time the fish remains in a polluted area. In this experiment, the sheepshead minnow accumulated the least amount of radioactive gold of any test organisms (fig. 2). The activity of the fish decreased during the latter stages of the experiment. A sloughing off of the epidermal mucous layer containing sorbed activity could account for the loss, or the physiological condition of the fish could have deteriorated and their rate of metabolism changed.

FIELD INVESTIGATIONS

The accumulation of radioactive gold released into the Cape Fear River was observed in both indigenous organisms and in caged organisms collected in Beaufort and maintained in the river. The investigations were coordinated with the release of radioactive gold which had been sorbed onto sediment particles.

The specific problem under investigation by the U.S. Army Corps of Engineers was to determine if sediment being deposited in the channels of the Cape Fear River, N.C., near the Sunny Point Army Piers near Southport, N.C., had been transported by currents from a spoil area on the opposite side of the river (U.S. Army Corps of Engineers, 1964). The answer was sought by tagging a small quantity of the sediment with gold 198, releasing this sediment in the spoil area, and tracing its distribution with an underwater scintillation probe mounted on a sled. The sediment was tagged by first forming a slurry into which 5 c. of gold 198 chloride were thoroughly mixed to allow maximum sorption. This was done in a special conical-bottomed container which served also as the release mechanism for the tagged sediment. The container floated in the water and was towed by boat over a predetermined course while the tagged sediment was being released. The entire procedure has been described in greater detail by Krone (1960).

Gold-tagged sediments were released at two different sites. The first 5 c. "drop" was made on October 24, 1962, at 6 p.m., at high tide, along an east-west line on the southern end of the Spoil area (fig. 4). A second 5 c. drop was made on the northern end of the spoil area on October 25 at 4 p.m., also at high tide. A water sample collected in the drop zone at this time had a


Andersons Landing
Ruins of Old Brunswick
Wilmington Beach
Ditch
Kure Beach
TANK
Peters Pt.
Reaves Pt.
Sunny Pt.
Federal Pt.
Governors Cr.
DROP LINE
DROP LINE
I
II
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spoil area
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Shoal
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VAR 4°00'W (1962)
ANNUAL INCREASE 4'
34°
54'
58'
marsh
piles
SOUTH RANGE
RED SECTOR

FIGURE 4.—Location of sampling stations and gold tracer drop zones in the Cape Fear River.

salinity of 24 °/oo, temperature of 18° C., and pH of 7.9.

Animals and sediment from the drop zone area were collected before and after the release of the labeled sediment. Samples of sediment and sea water, and of blue crabs; Atlantic croaker; star drum, *Stellifer lanceolatus:* flounder, *Paralichthys* sp.; and American menhaden, *Brevoortia tyrannus,* were collected 1 week prior to the first drop in order to measure background activity. Organisms and sediment were collected again on the third day following the release of the labeled sediment. In addition to those species collected before the release of labeled sediment, the white shrimp, *Penaeus setiferus*, appeared in samples taken after the release. Sediment samples from the drop zone were composed mostly of sand. Additional information on the sediments is given by the U.S. Army Corps of Engineers (1964).

Cages containing various estuarine organisms were placed at six stations around the proposed drop zone 24 hours before the scheduled release (fig. 4). Test animals at each station included 25 blue crabs; 50 oysters, *Crassostrea virginica;* and 50 mummichogs, *Fundulus heteroclitus*. Ten croakers were included at stations IV, V, and VI. The blue crabs were kept in separate cages to prevent predation on the other test animals. Also, at each station, plastic petri dishes filled with montmorillonite clay were placed in minnow traps to test for adsorption of gold 198. Five to ten animals of each species were removed from the cages for each sample.

The radioactivity content of the field samples was measured at the Bureau of Commercial Fisheries Radiobiological Laboratory, Beaufort, N.C., 110 miles from the sampling area. The detector system consisted of a 3-inch NaI(Tl) crystal coupled to a single-channel gamma spectrometer. Sediment and biological samples were placed in individual plastic bags, packed in an ice chest, and transported to the laboratory as soon as possible after sampling. Water samples were held in screw cap jars. If the water samples were found to be radioactive, the water was Millipore-filtered and counted again, along with the separated material, to determine whether the radioactive gold was associated with suspended material.

The various samples were measured for radioactivity in a manner that permitted the comparison of organisms, sediments, and water. To make these comparisons, it was necessary that the radioactivity in all of the samples be measured under similar conditions of geometry. Organisms containing gold 198 were measured for radioactivity before and after being dissolved in nitric acid and diluted to 900 ml. A factor was thus obtained for converting measurements made on the intact organisms to measurements which would be obtained after dissolving and diluting the organisms to 900 ml. A factor was obtained for the sediments in a similar manner, except that no acid was used and Calgon was added as a wetting agent. No preparation was necessary to measure gold 199 in the 900 ml. samples of water. Since radioactivity measurements in intact organisms and sediments could be converted to measurements based on their being contained in a 900-ml. volume of water, and since all measurements of water were for 900 ml., it was possible to compare activity contained in these three types of samples.

The radioactivity content of water, sediments, and biota varied widely between stations. Biological samples from stations III and VI did not contain measurable amounts of radioactivity at any time (table 5). As one would expect, biological samples from station II, located directly in the drop zone, contained higher concentrations of radioactivity than those of other stations. Lateral dispersion of radiogold was indicated by the increase in activity in the crabs and oysters from stations I and IV after 41 hours elapsed time.

The second application of gold appeared to have little or no effect on the levels of concentration in the samples, except perhaps those in station IV. Oysters and crabs accumulated radioactivity to maximum level 17 hours after the first radiogold

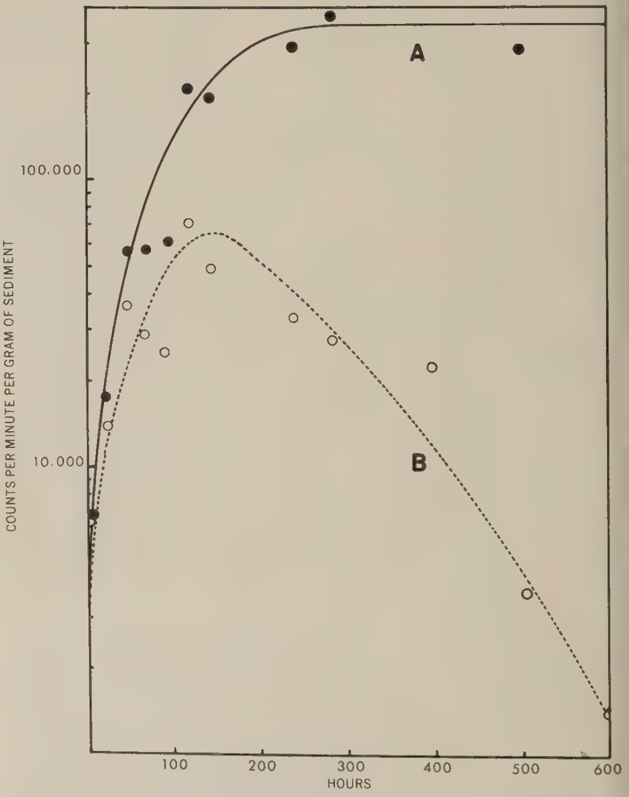

FIGURE 5.—Radioactivity content of biota and sediments from Cape Fear River after release of gold tracer.

application (fig. 5). However, this occurred 5 hours before the second application.

Background samples of biota and water collected in the drop zone area 1 week prior to the release of the labeled sediments did not contain measurable gamma activity in the energy range between 100 and 400 kiloelectron volts (Kev), the setting which includes the photopeak of radioactive gold. However, sediment samples contained gamma activity ranging from 367 to 729 counts per minute per kg. wet weight at this setting. Biota, water, and sediments collected from the same area 41 hours after the release did not show an increase in radioactive content over the background samples.

Table 5.—*Radioactive gold content of field samples* [1]

[Activity m.μc/kg.]

Elapsed time in hours	Sample	Station					
		I	II	III	IV	V	VI
1	Water	—	6.8	—	—	—	—
	Sediment	—	NS	—	—	—	—
	Fish	—	NS	—	—	—	—
	Oyster	—	23.8	—	—	—	—
	Clay	—	45.6	—	—	—	—
	Crab	—	27.3	—	—	—	—
17	Water	5.1	4.7	2.96	4.2	4.12	NS
	Sediment	NS	60.3	NS	—	NS	—
	Fish	NS	NS	NS	—	36.90	—
	Oyster	NS	70.9	NS	—	40.22	—
	Clay	NS	—	—	—	—	—
	Crab	NS	61.6	NS	—	—	—
41	Water	NS	NS	NS	NS	NS	NS
	Sediment	NS	NS	NS	NS	NS	NS
	Fish	NS	NS	NS	NS	NS	NS
	Oyster	15.7	31.1	NS	24.5	14.1	NS
	Clay	—	NS	—	—	—	—
	Crab	14.8	22.9	NS	24.9	19.0	—
144	Water	—	—	—	NS	—	NS
	Sediment	—	—	—	NS	—	NS
	Fish	—	—	—	NS	—	NS
	Oyster	—	—	—	NS	—	NS
	Crab	—	—	—	NS	—	NS

[1] NS indicates activity not significantly greater than background; dash indicates no sample was taken.

DISCUSSION

The potential hazards accompanying the release of radioactive material into the marine environment should be investigated so that the most dangerous situation possible is evaluated. The accumulation of radioactive gold from sea water by the animal community contained in the large tank was a simulation of this extreme situation: The closed system offered no opportunity for the animals to escape the contaminated area, and there was neither inflow of nonactive sea water nor outflow of contaminated water. Under these controlled conditions, organisms and sediments accumulated the isotope from sea water, with crabs and filter-feeding organisms accumulating the isotope to the greatest extent.

Surface sorption of radioactive gold, no doubt, is an important factor contributing to rapid accumulation by marine organisms and sediments. This is based on the observation that 50 percent of the isotope added to the water in an experimental environment moved very quickly to organisms and sediments within the tank. It is known that biological accumulation of a radiosotope by sorption occurs rapidly. Further, it has been shown that gold occurs in sea water in a particulate state. Since particles have difficulty passing through biological membranes, surface sorption is most important in their accumulation by marine organisms. The importance of surface sorption in the accumulation of radioactive gold by organisms was demonstrated experimentally when the radioactive content of clams buried in sediment was shown to be less than that of clams resting on the smooth bottom surface of the tank. Although the buried clams had less area exposed, the same average amount of water should have passed through their siphons as through the siphons of those resting on the bottom. If all the accumulation of gold had been a result of metabolism, the gold content of buried and exposed organisms should have been the same.

The literature contains several references pertaining to the surface accumulation of material from sea water. As early as 1937, Harvey demonstrated that particulate matter such as ferric hydroxide was associated with phytoplankton cells by electrostatic attraction to external surfaces. Also, Goldberg (1952) observed that particulate and colloidal iron was utilized by *Asterionella japonica*. Rice and Willis (1959) showed that particulate cerium 144 became attached to *Nitzschia* cells as a result of particles and cells coming in contact with each other and sticking.

The distribution of this isotope within the animals was observed by placing large quantities of radioactive gold directly into the gut of several estuarine animals. Those organs associated with excretion retained more gold 199 than did others, suggesting that the gold was simply being excreted rather than being stored or utilized. The principal route of gold administered as an oral dose to mammals was reported by Spector (1956) to be directly from the alimentary tract to the feces with little absorption along the way. In the present study, little, if any, radioactive gold was found in the organs of fish that were fed this isotope sorbed onto clay.

In field studies, animals and sediment maintained in cages in the drop zone sorbed little activity. This could have been caused by the tremendous dilution by river water and strong currents, and to the short physical half-life of the gold isotope. Since it was demonstrated experimentally that the animals retained little activity from ingested labeled sediment particles, the initial accumulation of activity was perhaps from unbound gold that was not sorbed onto sediments in the mixing hopper but remained in the water phase of the slurry.

Since gold is not biologically essential and is not concentrated significantly by estuarine animals, the isotope gold 198, with its short physical half-life of 2.7 days, appeared to be a safe and effective tracer for following sediment movement. Even though as much as 5 c. of gold 198 were released in the Cape Fear River at one time, the maximum concentration found in any of the animals tested was 70.9×10^{-5} μc. per g. of oyster at station II (table 5). This is slightly in excess of the maximum permissible concentration (MPC) for gold 198 in water effluent released in an unrestricted area, i.e., 5×10^{-5} μc./ml. (Code of Federal Regulations, 1960). However, station II was purposely located in the drop zone so that the caged animals would be subjected to the most extreme conditions of contamination. There is no evidence now that radiation from the low levels of gold 198 involved in these investigations affected the biota.

ACKNOWLEDGMENTS

Thomas J. Price provided unpublished data on mollusks and George H. Rees furnished data on blue crabs. The U.S. Army Corps of Engineers and its consultant, R. B. Krone, cooperated and assisted.

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A GENERIC KEY TO THE PROTOZOEAN, MYSIS, AND POSTLARVAL STAGES OF THE LITTORAL PENAEIDAE OF THE NORTHWESTERN GULF OF MEXICO [1]

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ABSTRACT

An illustrated key presenting criteria for differentiating the stages and substages of Gulf of Mexico penaeid larvae (and post larvae) from comparable stages of the more common nonpenaeids is presented. A second key permits generic identification of penaeid protozoean, mysis, and postlarval stages. All genera are illustrated, and a table of important diagnostic characters is included.

Shrimp of the Family Penaeidae which support valuable commercial fisheries in the northwestern Gulf of Mexico are being studied comprehensively by fishery scientists at the Bureau of Commerical Fisheries Biological Laboratory in Galveston, Tex. To properly manage such fisheries, it is necessary to fully understand the dynamics of the shrimp populations upon which they depend. This capability requires, in turn, as complete a knowledge as possible of the life history of the species involved.

Studies of the early (planktonic) life history of the Gulf's commercially important shrimps have been hampered by difficulties encountered in distinguishing larvae of these species from those of lesser importance. Fortunately, there has been considerable research on the description and general systematics of larval and postlarval Penaeidae both in this country and abroad. As a result, all the littoral genera known to occur in the northwestern Gulf of Mexico have had representatives—although not necessarily of indigenous species—at least partially described. The principal problem, therefore, was one of consolidating all the available information and ascertaining what portions of it might help describe the local penaeid larvae. The intent of this paper is to present criteria that will aid in distinguishing larvae and postlarvae of the genus *Penaeus* Fabricius from those of *Parapenaeus* Smith, *Sicyonia* H. Milne Edwards, *Solenocera* Lucas, *Trachypeneus* Alcock, and *Xiphopeneus* Smith, the five other littoral genera found locally.

The material made available for examination during this study was collected systematically between March 1959 and March 1960 and during January to December 1961. From January to September 1961, plankton was sampled with a Gulf-V net to depths of 45 fathoms between Cameron, La., and Freeport, Tex. In September, the sampling program was enlarged to include the area between Morgan City, La., and the mouth of the Colorado River, Tex.

Although various larval stages of several species represented in this area had been recorded, there were no established criteria for differentiating the penaeid larvae. Consequently, as new or theretofore unrecognized penaeid larvae and postlarvae were found in the plankton samples, they were assigned a code number and a reference sketch of them was made. Through the use of descriptions

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taken from the literature, and by comparison with larvae reared in the laboratory from eggs of known parentage, planktonic larvae were assigned to genera. Subsequent examination of accumulated material revealed the presence of protozoeal, mysis, and postlarval characters which remained constant within each genus. These characters were, in turn, used as criteria to construct a key to local genera. A key based for the most part on planktonic rather than laboratory-reared material has its limitations, but the scarcity of information concerning penaeid larvae from this area nevertheless justifies its presentation at this time.

Despite the fact that *Penaeus aztecus* Ives (brown shrimp); *P. duorarum* Burkenroad (pink shrimp); *Sicyonia brevirostris* (Stimpson) and *S. dorsalis* (Kingsley) (rock shrimps); *Trachypeneus similis* (Smith); and *Xiphopeneus krøyeri* (Heller) (seabob) have been reared successfully through the nauplial stage under laboratory conditions, the nauplii were found to be so similar as to defy attempts to fit them into a key. Although differences in setation are minor or absent, the lack of a dorsal protuberance (fig. 1f), as well as larger relative size, serves to distinguish nauplii of the genus *Penaeus*. In genera other than *Penaeus*, this protuberance is present on the dorsal surface of the body above the insertion of the second antennae.

Within a given developmental stage (e.g., Nauplius II, Protozoea I, etc.), the size ranges of penaeid larvae as a whole are extremely variable, although in the northern Gulf, larvae of the genus *Penaeus* are generally larger than those belonging to comparable stages of other genera. Hudinaga (1942) found that the protozoeal stages of *P. japonicus* Bate exhibited intermolt growth, the occurrence of which may also be true for other stages as suggested for nauplii of *Xiphopeneus krøyeri* by Renfro and Cook (1963). The possibility also exists that larvae (and postlarvae) of the same species grow dissimilarly at different times of the year. Since the relative size at each stage overlaps considerably between, as well as within, the various genera, it should be used with discretion for purposes of identification.

While the number of substages in each penaeid larval stage described in the literature has been found to vary, the normal situation in the northwestern Gulf of Mexico—as ascertained from material in plankton collections—seems to be five nauplial, three protozoeal, and three mysis substages. Examples of departure from this sequence are provided by the larvae of *Sicyonia brevirostris* which, when reared in the laboratory, appeared to pass through four mysis substages, and by those of *Parapenaeus* sp. which, as determined from sample material, also have at least four. Such apparent anomalies suggest that descriptions of penaeid larvae obtained either from rearing experiments or plankton samples must be viewed with caution until more is known of the effects of environmental factors on early growth and morphology.

Table 1, in addition to presenting the principal diagnostic characters included in the following key, also furnishes other valuable characters for distinguishing larvae and postlarvae.

All illustrations are intended to clarify generic characteristics and do not represent particular species.

KEY TO STAGES AND SUBSTAGES OF PENAEID LARVAE AND EARLY POSTLARVAE

1 Body simple, unsegmented; three pairs of appendages arising from anterior portion of body, first unbranched, second and third branched; paired caudal spines arise from posterior end of body (Nauplius) -------------------------- 2

Not as above -------------------------------- 7

2(1) Body pear shaped; pairs of caudal spines of equal length, extending straight posteriorly; lateral setae on appendages arise singly or in pairs; appendages lack spines or processes such as would be utilized for feeding purposes; carapace present only as a close-fitting rudiment in later stages (Penaeid nauplius fig. 1) -------------------- 3

One or more of the following characters present: body elliptical; pairs of caudal spines of unequal length or extending medianly, crossing one another; lateral setae on appendages arising in clusters; spines or processes such as would be utilized for feeding purposes present; a well-developed or prominent carapace present
Nonpenaeid nauplius

3(2) Five setae on exopod of second antenna; one pair of caudal spines; surface of body between insertion of caudal spines convex -- Nauplius I (fig. 1a)

More than five setae on exopod of second antenna; one or more pairs of caudal spines; surface of body between insertion of caudal spines not convex ------------------------------------ 4

4(3) Six setae on exopod of second antenna; usually one, sometimes two, pairs of caudal spines; surface of body between insertion of caudal spines flat -------------------- Nauplius II (fig. 1b)

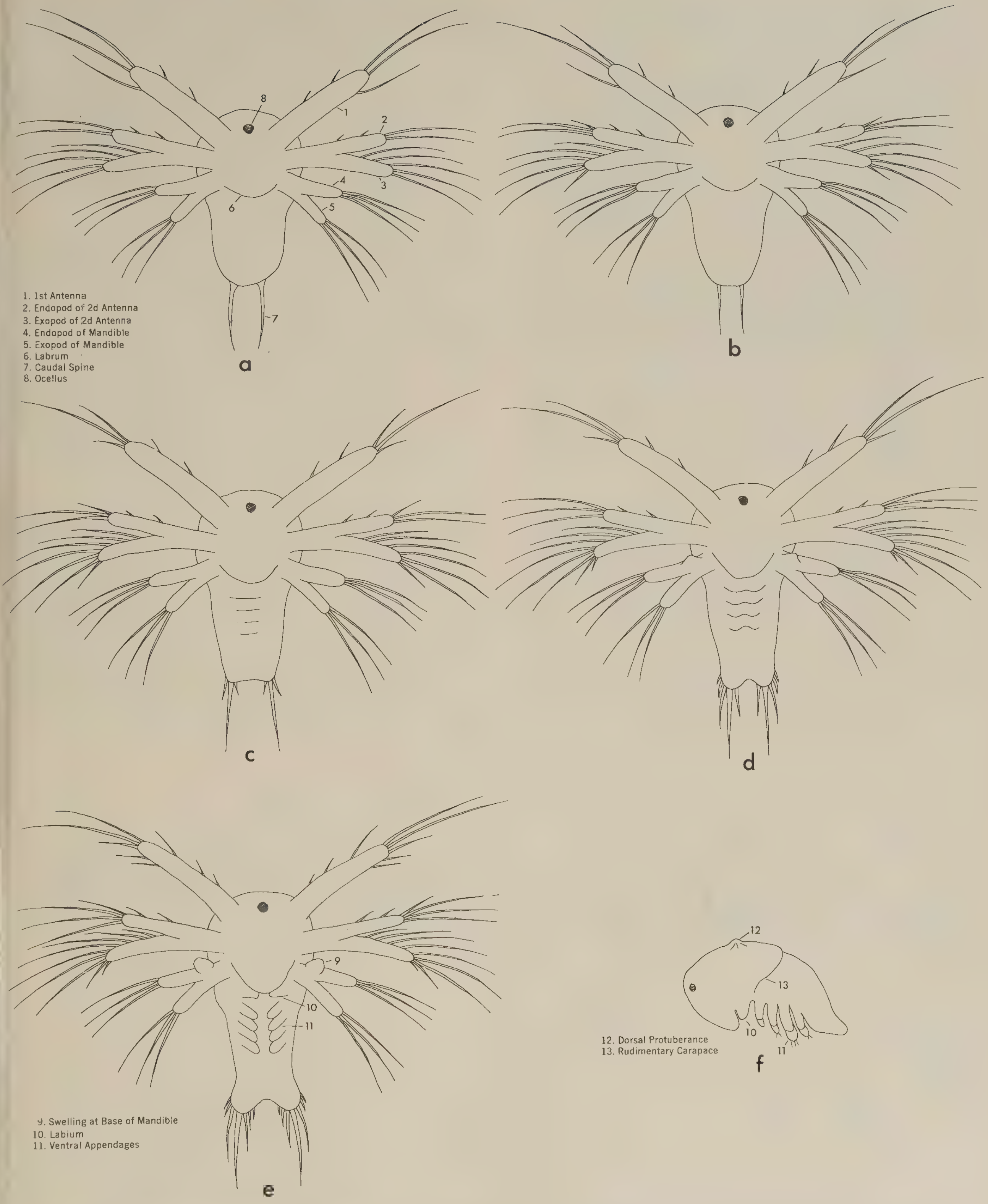

8
1
2
3
4
5
6
7
1. 1st Antenna
2. Endopod of 2d Antenna
3. Exopod of 2d Antenna
4. Endopod of Mandible
5. Exopod of Mandible
6. Labrum
7. Caudal Spine
8. Ocellus
a
b
c
d
9
10
11
9. Swelling at Base of Mandible
10. Labium
11. Ventral Appendages
e
12
13
10
11
12. Dorsal Protuberance
13. Rudimentary Carapace
f

FIGURE 1.—Penaeid nauplii: *a*, Nauplius I; *b*, Nauplius II; *c*, Nauplius III; *d*, Nauplius IV; *e*, and *f*, Nauplius V.

More than six setae on exopod of second antenna; usually three or more pairs of caudal spines; surface of body between insertion of caudal spines concave ---------- 5

5(4) Seven setae on exopod of second appenadge; usually three, sometimes four, pairs of caudal spines; surface of body between insertion of caudal spines slightly concave; no swelling at base of mandible ---------- Nauplius III (fig. 1c)

More than seven setae on exopod of second antenna; usually more than four pairs of caudal spines; surface of body between insertion of caudal spines deeply concave; base of mandible swollen ---------- 6

6(5) Eight setae on exopod of second antenna; usually five, sometimes six, pairs of caudal spines; slight swelling at base of mandible; endopod of mandible never transparent; rudimentary ventral appendages posterior to third appendages
Nauplius IV (fig. 1d)

Nine setae on exopod of second antenna; usually seven, sometimes six, pairs of caudal spines; large subconical protuberance at base of mandible; endopod of mandible frequently transparent; ventral appendages prominent
Nauplius V (fig. 1e)

7(1) Large, prominent, carapace followed by a slender segmented thorax and an abdomen which may or may not be segmented; two pairs of prominent appendages arising from anterior portion of body, the first unbranched, the second branched; prominent labrum present (Protozoea) ---------- 8

Not as above ---------- 11

8(7) Carapace does not completely cover thorax; abdomen bifurcate posteriorly, with each furca bearing at least seven spines; biramous first and second maxillipeds well developed, the third absent or present only as a rudiment; usually, no spines arise from posterior half of carapace; if spines present, a dorsal organ (fig. 2d) is present (Penaeid protozoea fig. 2) ---------- 9

One or more of the following characters present: carapace completely covers thorax; abdomen not bifurcate; caudal furcae bear less than seven pairs of spines; first and second maxillipeds not well developed or third maxilliped well developed; if numerous spines arise from posterior portion of carapace, dorsal organ not present
Nonpenaeid protozoea

9(8) Eyes sessile, beneath carapace; pereiopods absent; abdomen unsegmented
Protozoea I (fig. 2a)

Eyes stalked; pereiopods present at least as small buds; abdomen segmented ---------- 10

10(9) Uropods not present externally, may be seen beneath cuticle; pereiopods present only as small buds; first five abdominal segments without dorsal spines ---------- Protozoea II (fig. 2b)

Uropods present externally; pereiopods rudimentary, but biramous and prominent; first five abdominal segments with dorsal spines
Protozoea III (fig. 2c)

11(7) Carapace closely fitting with a rostrum that extends anteriorly between the eyes; five pairs of biramous pereiopods present, with the exopods elongate and bearing numerous setae which make them appear brushlike; six-segmented abdomen followed by telson and biramous uropods; pleopods, if present, rudimentary and nonfunctional (Mysis) ---------- 12

Carapace closely fitting with a rostrum extending anteriorly between the eyes; five pairs of pereio-

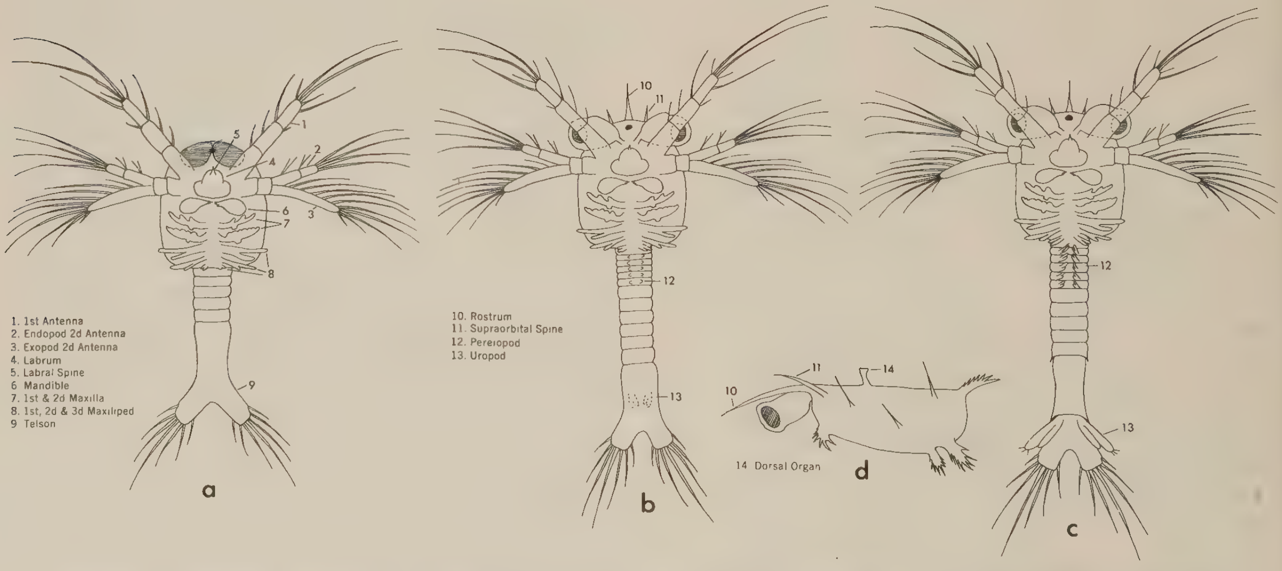


FIGURE 2.—Penaeid protozoeae: *a*, Protozoea I; *b*, Protozoea II; *c*, Protozoea III; *d*, Protozoea III, carapace.

pods present, with exopods absent or present only as rudiments; six-segmented abdomen followed by telson and biramous uropods; five pairs of setose, functional pleopods present (Postlarvae)---------------------------------- 15

12(11) First three pairs of pereiopods cleft to form rudimentary chelae; pleura of first abdominal segment overlap second; antennal blades present; pleopods develop on first five abdominal segments simultaneously although they are not necessarily of equal length; telson narrow and notched medianly; uropods without statocysts; usually, no spines originate from posterior half of carapace and margins of carapace not serrate; if spines or serrations present, a dorsal organ also present (Penaeid mysis fig. 3)---------------------- 13

One or more of following characters present: first three pereiopods not cleft to form rudimentary chelae; pleura of second abdominal segment overlap first; antennal blades absent; pleopods may not be present on all abdominal segments; telson broad and fan shaped or not notched medianly; uropods with statocyst; spines originate from posterior half of carapace or margins of carapace serrate, with no dorsal organ present-------------------- Nonpenaeid mysis

13(12) Pleopods absent-------------- Mysis I (fig. 3a)

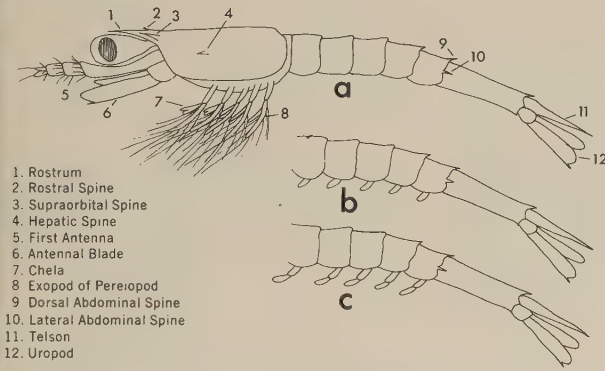
Pleopods present--------------------------- 14

14(13) Pleopods small and unjointed-- Mysis II (fig. 3b)

Pleopods long and jointed--- Mysis III (fig. 3c)

15(11) First three pairs of pereiopods chelate; pleura of first abdominal segment overlapping second; five pairs of functional pleopods present; gills covered by carapace; antennal blades present Penaeid postlarva (fig. 4)

One or more of the following characters present: first three pairs of pereiopods not chelate; pleura of second abdominal segment overlapping first; less than five pairs of functional pleopods present; gills extending from beneath carapace; antennal blades absent----------- Nonpenaeid postlarva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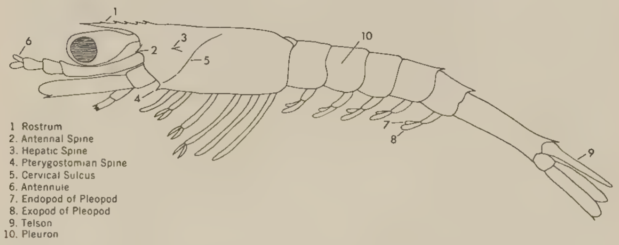
12
a
b
c
1. Rostrum
2. Rostral Spine
3. Supraorbital Spine
4. Hepatic Spine
5. First Antenna
6. Antennal Blade
7. Chela
8. Exopod of Pereiopod
9. Dorsal Abdominal Spine
10. Lateral Abdominal Spine
11. Telson
12. Uropod

FIGURE 3.—Penaeid myses: *a*, Mysis I; *b*, Mysis II; *c*, Mysis III.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1. Rostrum
2. Antennal Spine
3. Hepatic Spine
4. Pterygostomian Spine
5. Cervical Sulcus
6. Antennule
7. Endopod of Pleopod
8. Exopod of Pleopod
9. Telson
10. Pleuron

FIGURE 4.—Penaeid postlarva.

KEY TO GENERA OF PENAEID LARVAE AND POSTLARVAE

PROTOZOEAE

(Fig. 5)

1 Number of lateral setae on endopod of second appendage 1+1+2[2] ---------------- *Penaeus*
Number of lateral setae on endopod of second appendage not 1+1+2 ---------------------- 2

2(1) First appendage about twice as long as second; no spine on anterior margin of labrum; number of lateral setae on endopod of second appendage 1+2+3 ---------------------------- *Sicyonia*
First and second appendages of nearly equal length; a spine present on anterior margin of labrum; number of lateral setae on endopod of second appendage may be 1+2+3 ------------ 3

3(2) Number of lateral setae on endopod of second appendage 1+2+2, 1+2+3, or 2+2+2 - *Parapenaeus*
Number of lateral setae on endopod of second appendage not 1+2+2 or 2+2+2 -------------- 4

4(3) Number of lateral setae on endopod of second appendage 2+2+3 ----------------- *Solenocera*
Number of lateral setae on endopod of second appendage 2+2 -------------------------- 5

5(4) Four long, terminal setae on endopod of second appendage --------------------- *Trachypeneus*
Four long and one short terminal setae on endopod of second appendage --------------- *Xiphopeneus*

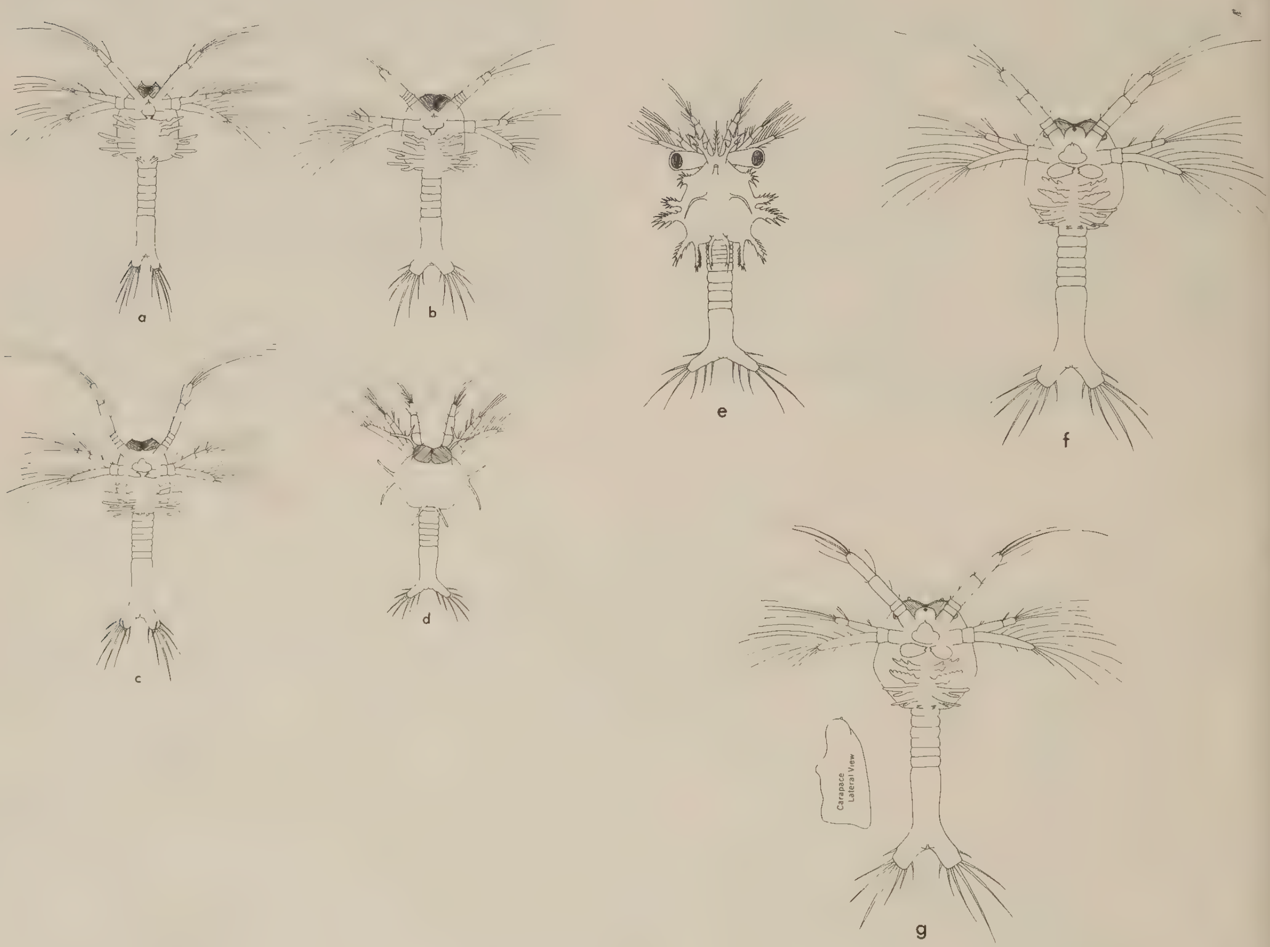

FIGURE 5.—Penaeid protozoeae: *a*, *Parapenaeus*, Protozoea I; *b*, *Penaeus*, Protozoea I; *c*, *Sicyonia*, Protozoea I; *d*, *Solenocera*, Protozoea I; *e*, *Solenocera*, Protozoea II; *f*, *Trachypeneus*, Protozoea I; *g*, *Xiphopeneus*, Protozoea I.

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[2] Starting with proximal seta, the number of lateral setae at each point of insertion is recorded.

MYSES

(Fig. 6)

1 Carapace and abdomen with many spines; dorsal organ present on dorsal surface of carapace ---- *Solenocera*
Carapace and abdomen without many spines; dorsal organ absent ---- 2

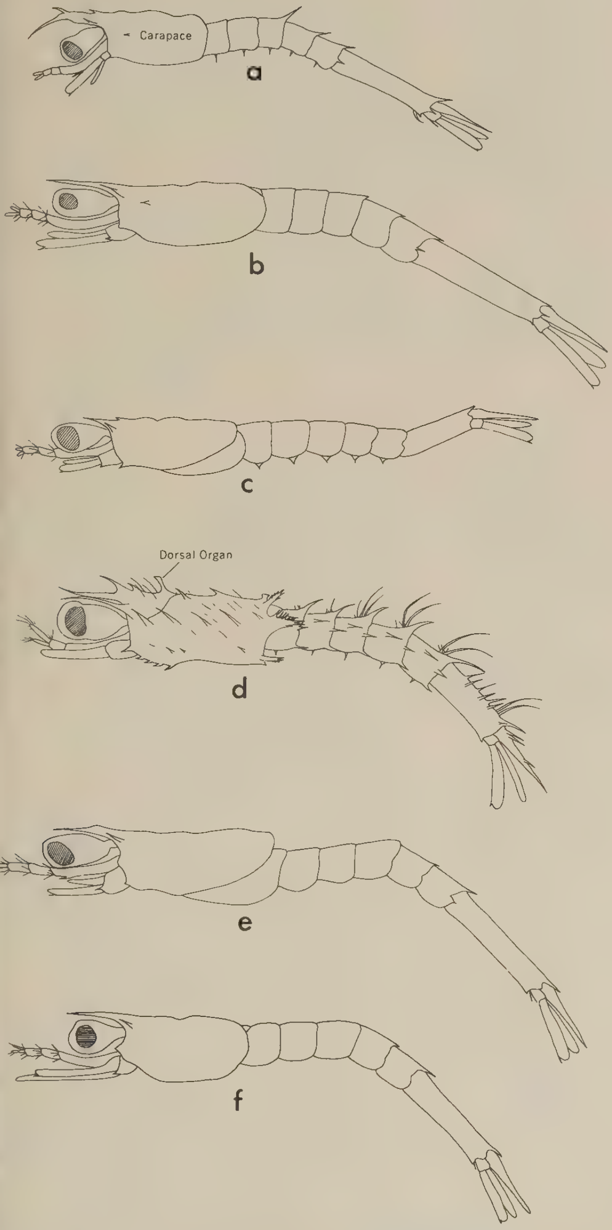

FIGURE 6.—Penaeid myses: *a, Parapenaeus,* Mysis I; *b, Penaeus,* Mysis I; *c, Sicyonia,* Mysis I; *d, Solenocera,* Mysis I; *e, Trachypeneus,* Mysis I; *f, Xiphopeneus,* Mysis I.

2(1) Dorsomedian spines not present on first five abdominal segments ---- *Sicyonia*
Dorsomedian spine present on at least fourth and fifth abdominal segments ---- 3

3(2) Dorsomedian spine not present on third abdominal segment ---- 4
Dorsomedian spine present on third abdominal segment ---- 5

4(3) Lateral spine present on fifth abdominal segment; rostrum shorter than eye ---- *Trachypeneus*
Lateral spine not present on fifth abdominal segment; rostrum as long as or shorter than eye ---- *Xiphopeneus*

5(3) Dorsomedian spine on third abdominal segment elongate ---- *Parapenaeus*
Dorsomedian spine on third abdominal segment not elongate ---- *Penaeus*

POSTLARVAE

(Fig. 7)

1 Total length 6.0 mm. or less[3] ---- 3
Total length greater than 6.0 mm ---- 2
2(1) Total length 6.0 mm. to 12.0 mm ---- 5
Total length 12.0 mm. to 25.0 mm ---- 10
3(1) No terminal spines on telson ---- *Sicyonia*
Terminal spines present on telson ---- 4
4(3) Medioterminal spines of telson longer than those adjacent to it ---- *Trachypeneus*
Medioterminal spine of telson equal in length to those adjacent to it ---- *Penaeus*
5(2) First abdominal segment with dorsal anteromedian spine ---- *Sicyonia*
First abdominal segment without dorsal anteromedian spine ---- 6
6(5) Pterygostomian spine present; pleopods of fifth abdominal segment with exopods and endopods of equal length ---- 7
Pterygostomian spine absent; pleopods of fifth abdominal segment with endopods inferior to exopods ---- 8
7(6) Antennules round; no cervical sulcus on carapace; rostrum curved ---- *Parapenaeus*
Antennules flattened; well-defined cervical sulcus present on carapace; rostrum straight ---- *Solenocera*
8(5) Antennal spine absent or minute; if present, subrostral teeth also present ---- *Penaeus*
Antennal spine very prominent; no subrostral teeth ---- 9
9(8) Rostrum shorter than eye ---- *Trachypeneus*
Rostrum longer than eye ---- *Xiphopeneus*
10(2) Rostrum usually with ventral teeth and shallowly compressed ---- *Penaeus*
Rostrum without ventral teeth and broadly compressed ---- 11
11(10) Pterygostomian spine present ---- 12
Pterygostomian spine absent ---- 13

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[3] Early *Xiphopeneus* postlarvae probably fall in the <6.0-mm. category, but none in this size range was noted during the study.

12(11) Antennules flattened; cervical sulcus present; sixth abdominal segment short and slightly curved - *Solenocera*
Antennules round; cervical sulcus absent; sixth abdominal segment long and straight - - *Parapenaeus*
13(11) Rostrum longer than eye - - - - - - - - - *Xiphopeneus*
Rostrum shorter than eye - - - - - - - - - - - - - - - - - 14
14(13) First abdominal segment with anteromedian spine on dorsal surface; sixth abdominal segment short - *Sicyonia*
First abdominal segment without anteromedian spine on dorsal surface; sixth abdominal segment elongate - *Trachypeneus*

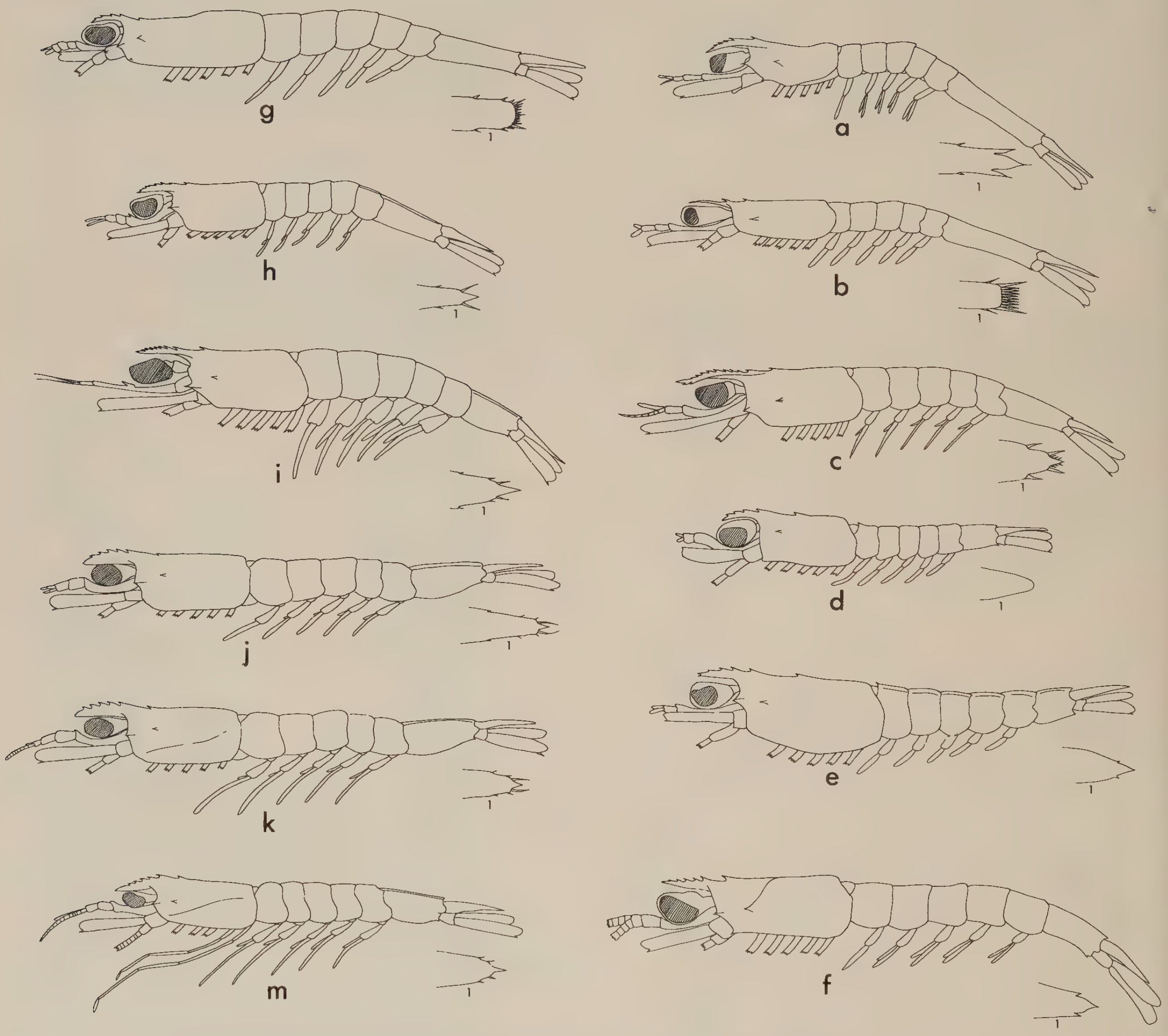

FIGURE 7.—Penaeid postlarvae: *a*, *Parapenaeus* postlarva, 8.0 mm.; *b*, *Penaeus* postlarva, 6.0 mm.; *c*, *Penaeus* postlarva, 15.0 mm.; *d*, *Sicyonia* postlarva, 5.0 mm.; *e*, *Sicyonia* postlarva, 14.0 mm.; *f*, *Solenocera* postlarva, 7.0 mm.; *g*, *Trachypeneus* postlarva, 6.0 mm.; *h*, *Trachypeneus* postlarva, 10.0 mm.; *i*, *Trachypeneus* postlarva, 25.0 mm.; *j*, *Xiphopeneus* postlarva, 6.0 mm.; *k*, *Xiphopeneus* postlarva, 7.5 mm.; *m*, *Xiphopeneus* postlarva, 12.0 mm.; *l*, Tip of telson.

TABLE 1.—*Characters of diagnostic importance in distinguishing genera during the early life history stages of the littoral Penaeidae occurring along the northern Gulf coast*

Stage and structure	*Parapenaeus*	*Penaeus*	*Sicyonia*	*Solenocera*	*Trachypeneus*	*Xiphopeneus*
PROTOZOEAE–GENERAL						
Relative lengths of 1st and 2d appendages.	Approximately equal.	Approximately equal.	First about twice as long as second.	Approximately equal.	First about 1½ as long as second.	First about 1½ as long as second.
Spine on labrum	Small	Small	Absent	Very long	Small	Small.
Telson	Narrow and deeply notched.	Medium width and notch.	Medium width and notch	Wide and shallowly notched.	Medium width and notch.	Medium width and notch.
Dorsal surface of carapace	Smooth	Smooth	Small hump	Spines and dorsal organ.	Small hump	Small hump.
Setation of endopod of second appendage.	Variable	1+1+2 lateral	1+2+3 lateral	2+2+3 lateral	2+2 lateral, 4 terminal.	2+2 lateral, 5 terminal.
PROTOZOEAE I						
Projection on front of carapace.	Pointed	Round	Round	Pointed	Round	Round.
Third maxilliped	Small, biramous, no setae.	Absent or present as small uniramous bud.	Small, biramous, no setae.	Small, biramous, with setae.	Small, biramous, with setae.	Small, biramous, with setae.
Spines on carapace	None	None	None	Four pairs	None	None.
PROTOZOEAE II						
Rostrum	Long	Long	Short	Long	Long	Long.
Supraorbital spines	Two pairs	One pair	Absent	One pair with many branches.	Absent	Absent.
PROTOZOEAE III						
Rostrum	Long	Long	Short	Long	Long	Long.
Supraorbital spines	One pair	One pair	Absent	One pair	Absent	Absent.
Dorsomedian spines of abdomen.	Present on six segments.	Present on first five segments.	Present on first five segments.	Present on first five segments.	Present on first five segments.	Present on first five segments.
Posterolateral spines of abdomen.	Present on fourth, fifth, and sixth segments.	Present on fifth and sixth segments.	Present on fifth segment.	Present on sixth segment	Present on fifth and sixth segments.	Present on fifth and sixth segments.
Ventrolateral spine on sixth segment.	One pair	One pair	One pair	One pair	Two pairs	Two pairs.
MYSIS						
Rostrum	Elongate, toothed, broadened at base.	Elongate, smooth, not broadened at base.	Short, toothed, not broadened at base.	Elongate, toothed, not broadened at base.	Elongate, toothed, not broadened at base.	Elongate, toothed, not broadened at base.
Superaorbital spine	Present	Present	Present	Present	Present	Present.
Hepatic spine	Present	Present	Absent	Present	Absent	Absent.
Ventromedian spines of abdomen.	Present	Absent	Present	Present	Absent	Absent.
Posterolateral spines of abdomen.	Present on fifth and sixth segments.	Present on fifth and sixth segments.	Absent	Present on first five segments.	Present on fifth segment.	Absent.

TABLE 1.—*Characters of diagnostic importance in distinguishing genera during the early life history stages of the littoral Penaeidae occurring along the northern Gulf coast*—Continued

Stage and structure	*Parapenaeus*	*Penaeus*	*Sicyonia*	*Solenocera*	*Trachypeneus*	*Xiphopeneus*
PROTOZOEAE—Continued						
MYSIS—Continued						
Dorsomedian spines of abdomen.	Present on third, fourth, fifth, and sixth segments. Spine of third segment elongate.	Present on third, fourth, fifth, and sixth segments.	Present on sixth segment only.	Present on six segments.	Present on fourth, fifth, and sixth segments.	Present on fourth, fifth, and sixth segments.
POSTLARVAE						
First TO 6.0-MM. POSTLARVAE:						
Rostrum	[First postlarva begins at about 8.0 mm.]	Straight	Curved	[First postlarva begins at about 7.0 mm.]	Curved	None examined.
Anteromedian spine on first abdominal segment.	-----	Absent	Present	-----	Present	
Sixth abdominal segment	-----	Elongate	Short	-----	Elongate	
6.0- TO 12.0-MM. POSTLARVAE:						
Anteromedian spine of first abdominal segment.	Absent	Absent	Present	Absent	Absent	Absent.
Length of pleopods	All equal	All equal	Fifth pleopod shorter than first.	Fifth pleopod shorter than first.	All equal	All equal.
Relative lengths of endopod and exopod of fifth pelopod.	Approximately equal.	Endopod absent or inferior.	Endopod absent	Approximately equal.	Endopod inferior	Endopod inferior, exopod elongate.
Pterygostomian spine	Present	Absent	Absent	Present	Absent	Absent.
Antennal spine	Present	Absent	Present	Present	Present	Present.
Antennules	Round	Round	Round	Flattened	Round	Round.
Sulcae of carapace	Absent	Absent	Absent	Cervical sulcus	Absent	Branchio-cardiac sulcus.
Rostrum	Curved, elongate	Straight, elongate	Straight, short	Straight, short	Curved, short	Curved, elongate.
Sixth abdominal segment	Elongate, straight	Elongate, straight	Short, straight	Medium, curved ventrally.	Medium, straight	Medium, straight.
12.0- TO 25.0-MM. POSTLARVAE:						
Rostrum	Curved, elongate, subrostral teeth absent.	Curved, elongate, subrostral teeth present.	Straight, short, subrostral teeth absent.	Straight, medium, subrostral teeth absent.	Curved, medium, subrostral teeth absent.	Curved, elongate, subrostral teeth absent.
Pterygostomian spine	Present	Absent	Absent	Present	Absent	Absent.
Antennules	Round	Round	Round	Flattened	Round	Round.
Sulcae of carapace	Absent	Absent	Absent	Cervical sulcus	Absent	Branchio-cardiac sulcus.
Sixth abdominal segment	Elongate, straight	Elongate, straight	Short, straight	Medium, curved ventrally.	Medium, straight	Medium, straight.
Anteromedian spine on first abdominal segment.	Absent	Absent	Present	Absent	Absent	Absent.

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Ray S. Wheeler and Robert F. Temple offered many helpful suggestions during the course of this study, and Daniel Patlan assisted with the drawings.

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MIGRATIONS AND GEOGRAPHIC DISTRIBUTION OF PINK SHRIMP, *PENAEUS DUORARUM*, OF THE TORTUGAS AND SANIBEL GROUNDS, FLORIDA [1]

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BUREAU of COMMERCIAL FISHERIES BIOLOGICAL FIELD STATION, MIAMI, FLA.

ABSTRACT

Pink shrimp, *Penaeus duorarum*, frequent the estuarine waters of south Florida as juveniles. As adults, they support valuable fisheries on the offshore Tortugas and Sanibel trawling grounds in the Gulf of Mexico. To study the Tortugas and Sanibel shrimp stocks as biological units, 15 mark-recovery experiments in which biological stains were the marking agents were made. These experiments (1) indicated timing and direction of shrimp migrations; (2) delineated estuarine nursery grounds; and (3) outlined geographic ranges of Tortugas and Sanibel shrimp stocks.

Prior to migrating offshore, the length of time spent by juvenile pink shrimp in the nursery areas varies from about 2 to at least 6 months. In migrating from nursery areas, some shrimp travel at least 150 miles (nautical) before recovery on the offshore grounds. Although migration routes are broad, shrimp emanating from particular sections of the nursery grounds demonstrate distinct distributional patterns on the offshore grounds.

The nursery grounds of the Tortugas shrimp stocks include Florida Bay and estuaries extending at least as far north as Indian Key on the southwest coast of Florida. The nursery grounds of the Sanibel shrimp stocks are confined to the southwest coast of Florida and include estuaries extending at least from Indian Key north to Pine Island Sound.

The geographic ranges of the Tortugas and Sanibel pink shrimp stocks overlap in the nursery areas near Indian Key and in the offshore water between the two trawling grounds. Apparently, Tortugas shrimp do not migrate to the Sanibel grounds and migration from the Sanibel to the Tortugas grounds is minimal. The geographic distributions depicted may constitute minimums for two reasons: First, the absence of fishing effort in certain contiguous areas prevented observations which could extend the known distribution. Second, larval and postlarval pink shrimp may migrate to or from areas beyond the ranges frequented by Tortugas and Sanibel shrimp as juveniles and adults.

The migrations and geographic distribution of pink shrimp, *Penaeus duorarum*, supporting commercial shrimp fisheries on the Tortugas and Sanibel grounds, have not been described previously. These two fisheries, located in the Gulf of Mexico off the southwest coast of Florida, provide a total shrimp catch of about 18 million pounds (heads on) annually. Knowledge of pink shrimp movement and distribution both on and off the grounds will contribute to a more thorough understanding of this animal's biology and serve as a basis for management of this resource.

The catch on the Tortugas and Sanibel grounds consists primarily of maturing and adult pink shrimp. This species has a life history similar to other members of the genus *Penaeus*. As adults, the female pink shrimp extrude eggs in offshore waters. After hatching, the young shrimp pass through larval and into postlarval stages as they move toward the coast. Coastal shallows and estuaries, utilized as nursery grounds, furnish an ecological environment considered necessary for these shrimp during the early stages of their development. The shrimp gradually move off-

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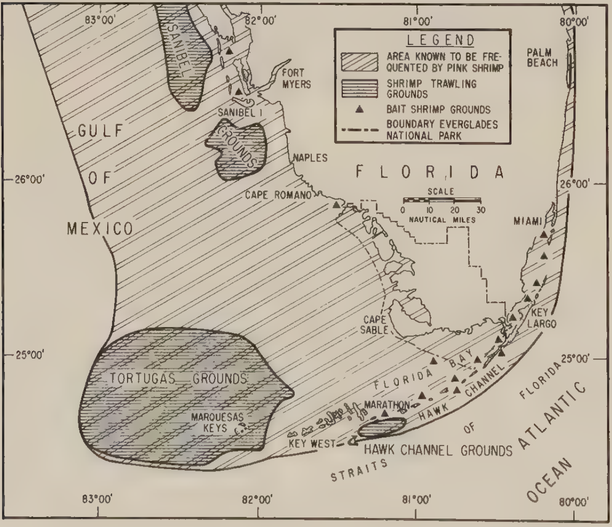
shore while maturing. The larger individuals eventually occupy the deeper waters (Iversen, Jones, and Idyll, 1960).

To study the Tortugas and Sanibel pink shrimp stocks as biological units, we must define the areas supporting these populations (or this population). This definition requires delineation of the shallows and estuaries that sustain young pink shrimp before they migrate to the Tortugas or Sanibel grounds, as well as the deeper, offshore waters frequented by the adult shrimp.

The extensive shallow waters surrounding and penetrating the southern portion of peninsular Florida and the adjoining Florida Keys support an abundance of juvenile pink shrimp, some of which are captured and sold as bait (fig. 1). Florida Bay, lying between the southern tip of Florida and the Florida Keys, is considered an important nursery area supplying pink shrimp to the Tortugas grounds (Iversen and Idyll, 1960). These nursery grounds may extend southwestward into the grassy shallows west of Marquesas Keys (Ingle, Eldred, Jones, and Hutton, 1959). Broad (1950) notes that "ample nursery grounds are to be found on the Florida west coast between Cape Sable and Cape Romano where the coastline is broken by numerous bays, creeks and rivers."

Maturing and adult pink shrimp are found in most offshore waters adjacent to south Florida, sometimes in depths of 60 fathoms [2] (Bureau of Commercial Fisheries, 1961 and 1962). On the Florida shelf, however, much of the bottom is too rough for conventional trawling gear. South of lat. 27°00′ N., the region under discussion, large pink shrimp are generally taken commercially only on the Sanibel, Tortugas, and Hawk Channel grounds where relatively smooth bottom can be found. Pink shrimp are fished commercially to a maximum depth of about 33 fathoms. The greater depths of the Straits of Florida, to the south and east of the Tortugas grounds, and the Gulf of Mexico, to the west, may serve as barriers to the migration of juvenile and adult pink shrimp.


83°00'
82°00'
81°00'
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LEGEND
▨ AREA KNOWN TO BE FREQUENTED BY PINK SHRIMP
▤ SHRIMP TRAWLING GROUNDS
▲ BAIT SHRIMP GROUNDS
BOUNDARY EVERGLADES NATIONAL PARK
SANIBEL
GROUNDS
FORT MYERS
SANIBEL I
PALM BEACH
GULF
OF
MEXICO
NAPLES
FLORIDA
CAPE ROMANO
SCALE
0 10 20 30
NAUTICAL MILES
MIAMI
26°00'
25°00'
CAPE SABLE
KEY LARGO
FLORIDA BAY
HAWK CHANNEL
TORTUGAS GROUNDS
MARQUESAS KEYS
MARATHON
KEY WEST
HAWK CHANNEL GROUNDS
STRAITS OF FLORIDA
ATLANTIC OCEAN

FIGURE 1.—Distribution of pink shrimp in the waters of south Florida.

In 1958, a total of 1,157 pink shrimp were tagged with Petersen disks and released near Flamingo in Everglades National Park. From this group, 1 tagged shrimp was recovered on the Tortugas grounds (Iversen and Idyll, 1960). Prior to this recovery no direct evidence linked small pink shrimp from south Florida estuaries to those larger shrimp supporting offshore fisheries. In addition, the relationship of pink shrimp occurring on the Hawk Channel and Sanibel grounds to the Tortugas pink shrimp was unknown. In 1958, the Bureau of Commercial Fisheries began a series of mark-recovery experiments in the waters of south Florida. One result of these experiments has been to demonstrate that certain shallow coastal waters are important contributors of recruits to the Tortugas and Sanibel shrimp fisheries. These experiments also outlined much of the range of the Tortugas and Sanibel pink shrimp stocks.

In studying pink shrimp, we were also concerned with the incidence of similar species that might be mistaken for pink shrimp. Two species closely related to pink shrimp have been reported from the waters of south Florida. These are *Penaeus brasiliensis* (Eldred, 1960) and *Penaeus aztecus* (Burkenroad, 1939; Tabb and Manning, 1961; Bureau of Commercial Fisheries, 1961). In Biscayne Bay and Hawk Channel, a relatively small number of *P. brasiliensis* were marked and released with *P. duorarum*. *P. brasiliensis* has not been noted from the Tortugas or Sanibel grounds despite examination of many shrimp from these areas. Two specimens of *P. aztecus* have been recorded from the northwest portion of the Sanibel grounds, but none from the Tortugas grounds.

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[2] Off the western edge of the Great Bahama Bank pink shrimp have been found in depths up to 200 fathoms (Bureau of Commercial Fisheries, 1961).

PROCEDURE

Design of Experiments

The experimental plan was based on the assumption that nursery grounds that furnish recruits to Tortugas and Sanibel pink shrimp populations are located in the estuaries and shallow marine waters of south Florida. To delineate these nursery areas and relate them to specific offshore shrimping grounds, young shrimp at selected coastal sites were captured, marked, and released near the point of original capture. Recovery of these marked shrimp on the Tortugas or Sanibel grounds established the affiliation of shrimp from a nursery area to those on the offshore grounds.

Inshore release sites were selected geographically near centers of juvenile shrimp abundance. At several of the selected locations, juvenile pink shrimp are plentiful only seasonally. Therefore, to obtain sufficient shrimp for marking, timing of inshore releases necessarily coincided with these estuarine peaks of abundance. Proceeding with marked shrimp releases according to these criteria, we established the affiliation of shrimp from shallow water areas along an extensive expanse of coastline to the offshore grounds.

Three offshore mark-recovery experiments, designed primarily to determine growth and mortality rates, also furnished information concerning migration and distribution of the larger pink shrimp.

Marked shrimp, which form the basis of this report, were stain-marked by injection of biological stains (Menzel), 1955; Dawson, 1957; Costello, 1964).

Recovery of Stained Shrimp

Shrimp fishermen and packers were informed of the purpose of mark-recovery experiments prior to each release of stain-marked shrimp. Preserved stain-marked shrimp in glass vials were displayed and posters describing stain-marked shrimp were placed in shrimp packing plants. For each recovery, together with the position, date and depth of recapture, rewards of from $1 to $5 were offered at various stages of the program.

Except for four recoveries made by Bureau of Commercial Fisheries vessels, all 2,201 of the marked shrimp recoveries which form the basis of this report were made by commercial fishing vessels. Inshore recoveries were made by bait shrimp fishermen in Biscayne Bay, Barnes Sound, and Florida Bay, and near Indian Key.

Stain-marked shrimp released offshore in or near areas where shrimp trawlers were active were caught and returned for reward payments in surprising numbers. Two groups released on the Tortugas grounds yielded 1,227 recoveries—21.1 percent of the first group released and 33.3 percent of the second group released. On Sanibel, 563 marked shrimp were recovered from a release of 2,496—a 22.5 percent recovery.

Inshore or estuarine releases were usually in localities remote from commercial fishing operations. This is reflected in recovery rates which averaged less than 1 percent of the numbers released.

Recovery rates are affected by factors such as the effective number of marked animals released—the number returned safely and in good condition to the environment from which captured. Also affecting recovery rates are direction of migration, location and amount of fishing effort, and awareness and interest of industry personnel in a position to recover marked shrimp. Some or all of these factors varied during the course of these experiments, and they have been considered in evaluating the data.

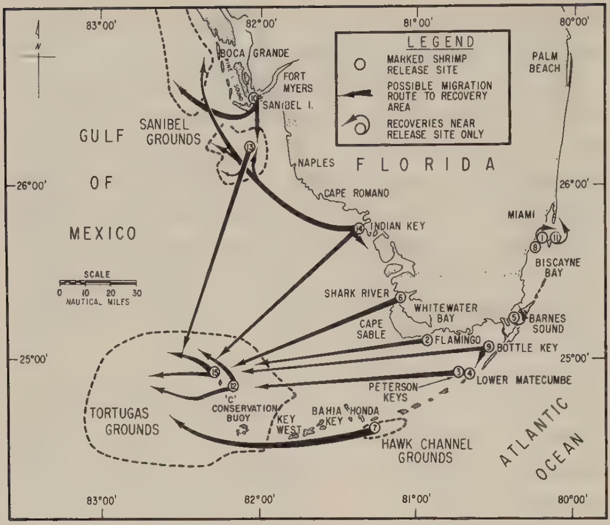
MIGRATIONS

Release and Recovery Sites

Table 1 summarizes pink shrimp mark-recovery experiments in south Florida waters from 1958 to 1963. Release sites are numbered in chronological order.

Figure 2 depicts the numbered release sites and general area of recovery of stain-marked shrimp. Arrows joining release and recovery sites do not necessarily indicate routes of migration.

On the southwest coast of Florida, marked juvenile pink shrimp released in large numbers in Pine Island Sound (10) migrated to the south and northwest portions of the Sanibel grounds but not to the Tortugas grounds. A release southeast of Sanibel, at Indian Key (14), resulted in recoveries near Indian Key and on both the Sanibel and Tortugas grounds. On the southwest coast of Florida and in Florida Bay, marked juvenile pink shrimp released near Shark River (6), Flamingo (2), Bottle Key (9), and Peterson Keys (3) were recovered in the Tortugas shrimp fishery. Several shrimp from Bottle Key were also caught in


83°00'
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N
LEGEND
MARKED SHRIMP RELEASE SITE
POSSIBLE MIGRATION ROUTE TO RECOVERY AREA
RECOVERIES NEAR RELEASE SITE ONLY
BOCA GRANDE
FORT MYERS
SANIBEL I.
PALM BEACH
GULF OF MEXICO
SANIBEL GROUNDS
NAPLES
FLORIDA
CAPE ROMANO
26°00'
MIAMI
INDIAN KEY
BISCAYNE BAY
SCALE
0 10 20 30
NAUTICAL MILES
SHARK RIVER
WHITEWATER BAY
CAPE SABLE
FLAMINGO
BARNES SOUND
BOTTLE KEY
25°00'
LOWER MATECUMBE
PETERSON KEYS
'C' CONSERVATION BUOY
KEY WEST
BAHIA HONDA KEY
TORTUGAS GROUNDS
HAWK CHANNEL GROUNDS
ATLANTIC OCEAN
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

FIGURE 2.—Release-recovery sites of marked pink shrimp in the waters of south Florida, 1958–63.

Florida Bay near and south of their release site, and one was recovered about 6 miles[3] north of the northern border of the Tortugas grounds. A few shrimp released at Bottle Key migrated at least 150 miles to the western portion of the Tortugas grounds.

On the southeast coast of Florida, young shrimp released in Biscayne Bay (1 and 11) and Barnes Sound (5) were recovered only near their respective release sites. No recoveries were reported from one release in Biscayne Bay (8) or from a small release at Lower Matecumbe Key (4), which borders eastern Florida Bay.

Migrations of adult shrimp were determined by releases in the deeper, offshore waters. Although a release of maturing shrimp on the south Sanibel grounds (13) resulted in 561 recoveries in the south Sanibel fishery, only two shrimp migrated to the Tortugas grounds. Marked shrimp released on two separate occasions on the Tortugas grounds near 'C' conservation buoy (12 and 15) apparently remained on or near the Tortugas grounds. The net movement of recovered individuals released on the Tortugas grounds was northwesterly into deeper water. Similar movement has been reported for tagged pink shrimp

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[3] Nautical miles are used in this report.

TABLE 1.—*Summary of pink shrimp mark-recovery experiments in south Florida waters, 1958–63*

Release site	Site number	Date of release	Released	Area of recovery	Recovered	Period of recovery	Days-out time [1]		
							Minimum	Maximum	Mean [2]
		1958	*Number*		*Number*		*Number*	*Number*	*Number*
Biscayne Bay	1	Apr. 24–May 29	19,358	Biscayne Bay	57	May–July 1958			(3)
Flamingo	2	Oct. 24–31	7,264	Tortugas grounds	4	Jan.–Feb. 1959	84	121	99
		1959							
Peterson Keys	3	Jan. 29	1,729	Tortugas grounds	11	Mar.–May 1959	46	93	69
Lower Matecumbe Key.	4	Mar. 6	1,672		0	No recoveries			
Barnes Sound	5	July 7–16	7,084	Barnes Sound	29	Aug. 1959–Jan. 1960.	16	174	73
Shark River	6	Nov. 2–6	16,638	Tortugas grounds	31	Dec. 1959–Mar. 1960.	35	126	81
		1960							
Hawk Channel	7	Feb. 4	6,815	Tortugas grounds	18	Mar.–May 1960	50	160	83
Biscayne Bay	8	Aug. 9	11,000		0	No recoveries			
Bottle Key	9	Nov. 1–4	13,306	Florida Bay	10	Nov. 1960–Jan. 1961.	22	80	31
				Tortugas grounds	50	Jan.–May 1961	72	205	124
Pine Island Sound	10	Nov. 29–Dec. 15	32,913	S. Sanibel grounds	149	Jan.–Nov. 1961	36	331	106
				NW. Sanibel grounds	6	Mar.–May 1961	112	160	135
		1961							
Biscayne Bay	11	Apr. 18	2,775	Biscayne Bay	4	May–June 1961	34	58	51
Tortugas grounds	12	Sept. 20–23	2,091	Tortugas grounds	443	Sept. –Dec. 1961	1	85	26
		1962							
Sanibel grounds	13	Mar. 19–22	2,496	Sanibel grounds	561	Mar.–Aug. 1962	1	146	33
				Tortugas grounds	2	July 1962	115	115	115
Indian Key	14	Aug. 27–Sept. 5	19,860	Indian Key	11	Sept. 1962	7	19	14
				S. Sanibel grounds	22	Oct. 1962–Apr. 1963.	53	229	159
				NW. Sanibel grounds	1	Nov. 1962	89	89	89
				Tortugas grounds	8	Oct. 1962–Mar. 1963.	40	185	128
Tortugas grounds	15	Dec. 11–15	2,350	Tortugas grounds	784	Dec. 1962–Mar. 1963.	1	106	21
Total			147,351		2,201				

[1] Calculated from the mean release date.
[2] Calculated from all recoveries.
[3] Widespread of release dates at site number 1 negates value of "days-out time" data.

released and recovered on the Tortugas grounds (Iversen and Jones, 1961). Another offshore release of stain-marked shrimp in Hawk Channel (7), south of Bahia Honda Key, yielded recoveries on the Tortugas grounds.

Areal Distribution

In figure 2 lines connecting release and recovery sites suggest possible migration routes traversed by pink shrimp en route to the Tortugas or Sanibel grounds. Actual routes of migration are not known because of the few recoveries in intervening areas which receive limited fishing effort. One exception pertains to the inshore leg of the route followed by shrimp released near Bottle Key as they moved toward the Tortugas grounds. From this group, a bait shrimp fisherman recovered 10 marked shrimp in Florida Bay 22 to 80 days after release. Of these 10, 7 were found near the release site, and 3 had moved southwest of Bottle Key toward a pass breaching the Florida Keys. Higman (1952) reported large catches of shrimp at such passes on night tides flowing from Florida Bay to the Atlantic Ocean. Undoubtedly, many shrimp from Florida Bay move into Hawk Channel, and we have now established that shrimp from the Hawk Channel grounds south of Bahia Honda Key migrate to the Tortugas grounds. Such movement was suggested by Costello and Allen (1960).

The distribution of recoveries from individual releases shows that migration routes may be broad and that shrimp disperse considerably while migrating. For example, shrimp released at Indian Key have been recovered at points as far as 125 miles apart. When there is a protracted departure time from a release site, such as occurred at Bottle Key (table 1), separate elements of the marked group may be subjected to a diverse environment (temperature, salinity, tides, currents) that could affect the direction of migration.

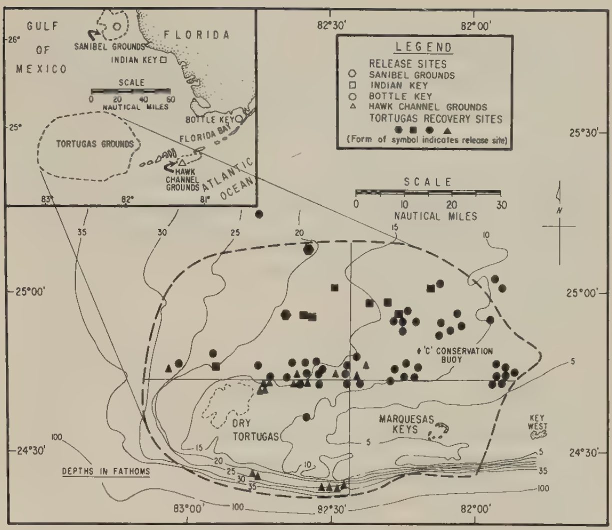
GULF OF MEXICO
FLORIDA
SANIBEL GROUNDS
INDIAN KEY
SCALE
0 20 40 60
NAUTICAL MILES
BOTTLE KEY
FLORIDA BAY
TORTUGAS GROUNDS
HAWK CHANNEL GROUNDS
ATLANTIC OCEAN
26°
25°
83°
82°
81°
82°30'
82°00'
LEGEND
RELEASE SITES
○ SANIBEL GROUNDS
□ INDIAN KEY
○ BOTTLE KEY
△ HAWK CHANNEL GROUNDS
TORTUGAS RECOVERY SITES
● ■ ● ▲
(Form of symbol indicates release site)
SCALE
0 10 20 30
NAUTICAL MILES
N
25°30'
25°00'
24°30'
35
30
25
20
15
10
5
100
'C' CONSERVATION BUOY
DRY TORTUGAS
MARQUESAS KEYS
KEY WEST
DEPTHS IN FATHOMS
83°00'
82°30'
82°00'

FIGURE 3.—Distribution of recoveries of pink shrimp on the Tortugas grounds from four release sites.

On the Tortugas grounds, the size of pink shrimp increases with the depth (Iversen, Jones, and Idyll, 1960). In general, mark-recovery experiments also indicate that pink shrimp move into deeper water as they increase in size. Thus, from examining the depth contours, we would expect that the majority of recruits enter the Tortugas and Sanibel grounds from the shallower waters northeast, east, or southeast of the grounds. On the Tortugas grounds the recovery patterns of marked shrimp from a common release area suggest the directions from which the shrimp enter the grounds. Reference is made to figure 3, which illustrates the recovery positions on the Tortugas grounds of shrimp liberated at four release sites Because of varied fishing effort, the actual distributional pattern of marked individuals on the grounds may differ somewhat from that suggested by the recoveries. The greatest concentration of fishing pressure occurs in the northeast quadrant of the grounds followed, in descending order, by the northwest, southwest, and southeast quadrants. Fishing pressure in the southeast quadrant is minimal and probably few recoveries should be expected from there. Bearing these qualifications in mind and by inspecting figures 2 and 3, we made the following observations:

1. Recoveries of shrimp migrating from the Sanibel grounds (13) were confined to the northwest quadrant of the Tortugas grounds, suggesting entrance from the north.
2. Recoveries of shrimp migrating from Indian Key (14) were distributed within the northwest and northeast quadrants of the Tortugas grounds, indicating entrance from the north and northeast.
3. Recovery positions of shrimp migrating from Bottle Key (9) were concentrated in the northeastern and west central portions of the grounds. This recovery pattern may be distorted by the limited fishing effort in the southeast quadrant. Thus, indications are that Bottle

Key shrimp entered the Tortugas grounds from the east, and, perhaps, northeast and southeast.

4. Shrimp that migrated from Hawk Channel (7) were concentrated along the southern border and in the west central section of the Tortugas grounds. Once again, the distributional pattern may be distorted by limited fishing effort in the southeast quadrant. It appears, however, that Hawk Channel shrimp entered the grounds from the southeast.

On the south Sanibel grounds, distribution of the first 23 recoveries of marked shrimp released in Pine Island Sound indicates that these shrimp entered the grounds from the shallower waters to the northeast and east (fig. 4). A comparison of the distributional pattern of the last 23 recoveries with that of the first 23 indicates the general trend of movement was into deeper water, or southwestward on the south Sanibel grounds.

TIME DISTRIBUTION

The period of time expended by pink shrimp (1) on nursery grounds, (2) while traversing migration routes, and (3) on the offshore grounds can be approximated in some cases from the number of days elapsing between release and recovery of marked shrimp, or "days out time" (table 1). Recovery frequencies for half-month periods on the Tortugas and Sanibel grounds (fig. 5) indicate periods of availability of marked shrimp from various release sites. Caution in interpreting these data is necessary since not all shrimp of a marked group depart the release areas at the same time, are recovered immediately upon reaching the offshore grounds, or are recovered in proportion to their relative abundance.

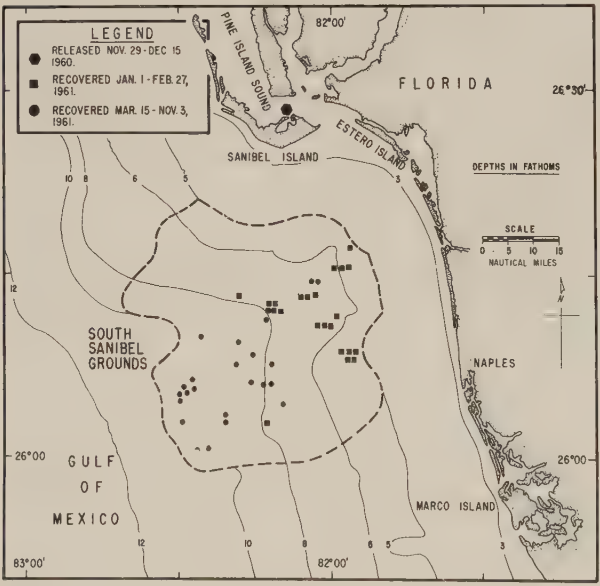

Figure 4.—Distribution of recoveries of pink shrimp on the south Sanibel grounds from releases in Pine Island Sound.

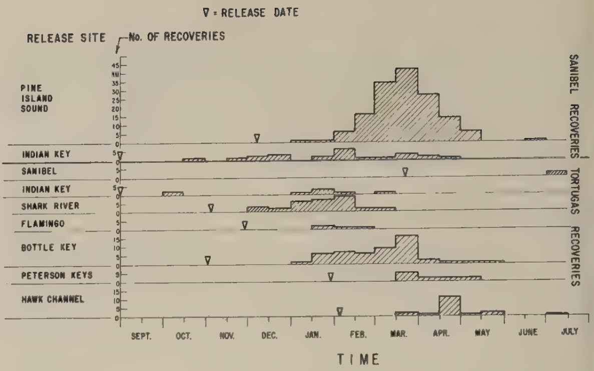

Figure 5.—Time-frequency distribution of marked shrimp recoveries on the Tortugas and Sanibel grounds by one-half-month periods.

A few pink shrimp that were marked and released in Barnes Sound (5) remained in the Sound for at least 174 days. Following the pink shrimp age-size relation given by Kutkuhn,[4] we estimated the smallest shrimp released, 16.0 mm. carapace length (75.0 mm. total length), to be about 60 days old. If 21–28 days are allowed for larval and early postlarval development prior to entrance into the nursery grounds, then it appears that under certain conditions more than 6 months of life may be spent in the estuaries. Conversely, time spent in the estuaries may be relatively brief. Only 35 days after the Shark River release (6), one marked male, 20.2 mm. carapace length (94.8 mm. total length), was recovered on the Tortugas grounds. Estimating this shrimp's age as 79 days and subtracting pre-estuarine entrance time, we found it apparently spent less than 2 months in the estuarine environment. The occurrence of pink shrimp less than 20.0 mm. carapace length (92.5 mm. total length) on the Tortugas grounds may indicate that some individuals spent little or no time on the more distant estuarine nursery grounds.

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[4] Kutkuhn, Joseph H., Dynamics of a penaeid shrimp population and management implications, p. 313, loc. cit.

Marked shrimp from the Bottle Key release (9), made in November 1960, were recovered in Florida Bay up to 80 days after release. One marked shrimp was recovered in the Bay after two other Bottle Key shrimp had already been caught on the Tortugas grounds. These recoveries show clearly that not all members of a given group of shrimp depart the estuaries at the same time. Bottle Key shrimp were recovered on the Tortugas grounds from January through May 1961 (fig. 5). The majority, however, were taken between January 16 and March 31, indicating that most of the marked Bottle Key shrimp that reached the Tortugas grounds were available for recapture within 75 to 149 days after release. The straight line distance between Bottle Key and 'C' conservation buoy, located near the center of fishing effort on the Tortugas grounds, is about 100 miles. Stained shrimp released in September 1961 (12) and December 1962 (15), near 'C' buoy on the Tortugas grounds, were recovered up to 85 and 106 days after release, respectively. During these periods, many had moved west or northwest into deeper water, some as far as 35 miles. Although several shrimp from release site 15 were taken just south of the northern border of the Tortugas grounds, none was recovered off the Tortugas grounds (fig. 6).

Marked shrimp released in Pine Island Sound (10) in November and December 1960, were recovered on the Sanibel grounds from January through November 1961. The center of the south Sanibel grounds is about 22 miles from the release site. The greatest numbers are recovered between February 1 and May 15. Part of the increase during this period, however, may be a reflection of increased fishing effort. One shrimp was recovered on the Sanibel grounds about 11 months after release. Since the smallest shrimp released was estimated to have been at least 1 month old, the recovered shrimp must have been at least a year old.

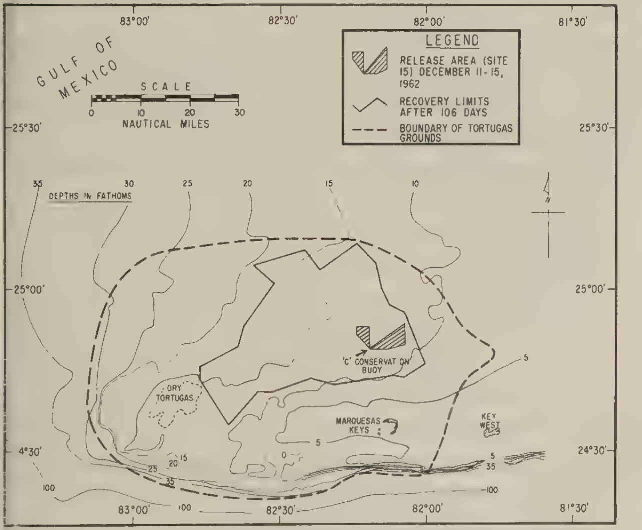


Figure 6.—Dispersal of marked pink shrimp on the Tortugas grounds, December 1962 through March 1963.

Marked pink shrimp released on the south Sanibel grounds (13) in March 1962 were caught there up to 146 days after release. The recovery positions indicated gradual movement into deeper water to the west and southwest. After 115 days two marked shrimp were caught on the northwestern Tortugas grounds, about 80 miles distant.

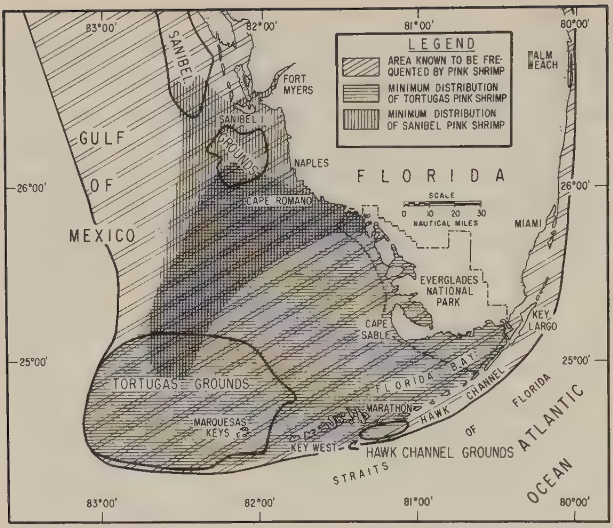
GEOGRAPHIC RANGE OF THE TORTUGAS AND SANIBEL PINK SHRIMP

The range and relationship of pink shrimp stocks of the Tortugas and Sanibel grounds were demonstrated by mark-recovery experiments. The Tortugas stocks of pink shrimp are defined as those pink shrimp that are available for capture on the Tortugas shrimp trawling grounds during some portion of their life. The Sanibel stocks may be similarly defined by appropriate word substitution. The sources of pink shrimp eggs and larvae that perpetuate these fisheries have not been positively established. Much of the area frequented by Tortugas (or Sanibel) pink shrimp as juveniles and adults, however, can be determined by inspection of marked shrimp release-recovery information (fig. 2 and table 1), Figure 7 is provisional and probably depicts only the minimum ranges of the Tortugas and Sanibel pink shrimp stocks.

Tortugas Stocks

The Tortugas trawling grounds, located northwest, west, and southwest of Key West, have a maximum depth of about 33 fathoms. The "boundary" is rather indefinite and encloses about 3,100 square miles. In much of the area trawling is restricted by rough bottom or extreme shallowness.

North, northeast, and east of the Tortugas grounds, the Tortugas stocks of pink shrimp


83°00'
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LEGEND
AREA KNOWN TO BE FREQUENTED BY PINK SHRIMP
MINIMUM DISTRIBUTION OF TORTUGAS PINK SHRIMP
MINIMUM DISTRIBUTION OF SANIBEL PINK SHRIMP
ALM EACH
SANIBEL
FORT MYERS
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GULF
OF
MEXICO
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26°00'
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0 10 20 30
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EVERGLADES NATIONAL PARK
KEY LARGO
CAPE SABLE
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TORTUGAS GROUNDS
FLORIDA BAY
HAWK CHANNEL
MARATHON
MARQUESAS KEYS
KEY WEST
HAWK CHANNEL GROUNDS
FLORIDA
OF
STRAITS
ATLANTIC
OCEAN

Figure 7.—Provisional ranges of Tortugas and south Sanibel pink shrimp stocks.

frequent an area extending at least to release sites 13, 14, 6, 2, 9, 3, and 7 (fig. 2). From the south section of the Sanibel grounds (13), two marked shrimp moved southward to the northwest portion of the Tortugas trawling area, establishing a degree of affiliation between these two fisheries. Because many juvenile shrimp released in Pine Island Sound (10) migrated to the Sanibel shrimp fishery, the relationship of Pine Island Sound shrimp to the Tortugas stocks is also indicated. A total of 35,409 marked shrimp released on Sanibel and in Pine Island Sound, however, yielded 716 recoveries in the Sanibel fishery and only two recoveries to the south, on the Tortugas grounds. Therefore, contribution of shrimp from these two northern sites to the Tortugas fishery must be considered minimal.

Indian Key (14) is about 55 miles southeast of Pine Island Sound. Juvenile pink shrimp from Indian Key are definitely affiliated with the Tortugas stocks, although almost three times as many marked shrimp released at Indian Key were recovered on the Sanibel grounds as on the Tortugas grounds. Analysis of recoveries from release sites 10, 14, and 6 suggests that the northward distribution of Tortugas pink shrimp along the Florida west coast ends north of Indian Key.

Southward from Indian Key to Shark River (6), Flamingo (2), and the Whitewater Bay-Florida Bay complex, we found the northeasterly penetration of the Tortugas pink shrimp stocks restricted by the land mass of the Florida peninsula, not by the coastline. For the Whitewater Bay drainage area, Tabb, Dubrow, and Jones (1962) presented evidence linking juvenile shrimp from estuaries upstream (inland) to the Tortugas population and to coastal release sites proven to be Tortugas affiliated.

The Tortugas pink shrimp recruitment range extends eastward at least to Bottle Key (9) and probably ends at the periphery of northeastern Florida Bay. Evaluation of the results of releases 6, 2, 9, 3, and 7 strongly indicates that all of Florida Bay provides recruits to the Tortugas fishery. Evidence that a separation of stocks may occur between Bottle Key and Barnes Sound (5) is indicated by the fact that considerably more marked shrimp were released in the Tortugas noncontributing areas northeast of Bottle Key than in the adjacent contributing areas to the southwest. A total of 40,217 marked shrimp was released in Biscayne Bay (1, 8, and 11) and Barnes Sound as compared to a total of 15,035 released near Peterson Keys (3) and Bottle Key. Recoveries in Barnes Sound were particularly interesting, because some marked shrimp were recovered near the release site more than 5½ months after release. The Biscayne Bay and Barnes Sound releases, however, occurred in late spring and summer, while the Peterson Keys and Bottle Key releases occurred in late fall and winter. The possibility cannot be discounted that migration patterns and, therefore, stock distribution may vary seasonally. More definitive results might be obtained from releases in both areas during the same season. However, marked shrimp releases at Bottle Key could not be seasonally timed to coincide with the prior release in Barnes Sound because pink shrimp occur in sparse quantities in northeastern Florida Bay during the summer.

The negative results of the Lower Matecumbe Key release (4) can possibly be attributed to a separation of stocks in that area, but are more likely a reflection of the relatively few (1,672) marked individuals released.

In the offshore waters east of the Tortugas grounds, the Tortugas pink shrimp recruitment range extends at least to that part of Hawk Channel (7) south of Bahia Honda Key. However, if shrimp from the Peterson Keys-Bottle Key area are found to use the adjacent Hawk

Channel as a route to the Tortugas grounds (migrations), the known limit of the Tortugas population would be extended northeastward on the Atlantic side of the Keys.

South, southeast, and east of Hawk Channel, pink shrimp have been caught in the Straits of Florida in depths to 60 fathoms (Bureau of Commercial Fisheries, 1961 and 1962). South of the Tortugas trawling grounds, pink shrimp have been taken in depths to 37 fathoms (Springer and Bullis, 1954). At these depths, however, pink shrimp have not been found abundant. The relationship of these "deep water" shrimp to those inhabiting the relatively shallow water of the Tortugas grounds has not been determined.

Sanibel Stocks

The Sanibel grounds comprise two distinct areas of trawlable bottom and are located northwest and south of Sanibel Island. Most trawling is confined to depths of less than 10 fathoms The southern boundary of the south Sanibel grounds is about 50 miles north of the Tortugas northern boundary (fig. 1). The northwest portion of the Sanibel shrimp grounds represents the southern extremity of a sporadic, undefined pink shrimp fishery which parallels a large portion of the Florida west coast.

Recoveries of marked shrimp reveal that Pine Island Sound serves as a nursery ground for both sections of the Sanibel grounds.

In this discussion the two Sanibel areas will be treated separately since there are indications that the northwest Sanibel grounds may support stocks of pink shrimp differing from those of the south Sanibel grounds. This is suggested by the fact that while 2,496 marked shrimp were released on south Sanibel (13), and 563 recovered there, none was recovered on northwest Sanibel despite moderate fishing effort in the latter area. One marked shrimp, however, from the Indian Key release (14) was recovered in the northwest Sanibel fishery. This shrimp very likely passed through the south Sanibel grounds en route to northwest Sanibel, linking all three areas. These apparently contradictory results may indicate that movement of shrimp from the southeast to northwest Sanibel is seasonal or sporadic. Because no marked shrimp have been released on northwest Sanibel, the relationship of shrimp from this area to shrimp stocks to the south is unknown.

The coastal distribution of shrimp recruited to the south Sanibel fishery extends from at least Pine Island Sound (10) to Indian Key (14). Juvenile shrimp recruited to the south Sanibel fishery probably issue from estuaries between and including these release sites. Since 22 of the marked shrimp released at Indian Key were recovered on the south Sanibel grounds, as compared with 8 on the Tortugas grounds, the southeastern limits of the south Sanibel shrimp population probably lie south of Indian Key but north of Shark River. The latter point is emphasized by the fact that releases of 16,638 marked shrimp at Shark River and 23,971 in Florida Bay have resulted in numerous recoveries on the Tortugas grounds but none on the Sanibel grounds.

The distribution of recoveries from coastal and offshore releases provides good evidence that the Tortugas and Sanibel shrimp stocks overlap in the general area of Indian Key (14) and offshore, between the Tortugas and Sanibel grounds. Two stain-marked shrimp, mentioned previously, migrated from the Sanibel to the Tortugas grounds, apparently crossing the intervening area. The bottom in this area is rough and usually precludes successful trawling with conventional shrimping gear. Despite low fishing effort in the area, two pink shrimp tagged and released on the Tortugas grounds were recovered 11 and 14 miles north of the present northern border of the Tortugas grounds (Iversen and Jones, 1961). In addition, one stain-marked shrimp from the Bottle Key release was recovered 6 miles north of the Tortugas border (fig. 3). There is no evidence, however, of migration from the Tortugas to the Sanibel grounds. Of 4,441 stain-marked shrimp released on the Tortugas grounds, none was recovered on or near Sanibel grounds. Because the movement of pink shrimp is generally into deeper water, migration from the Tortugas grounds to the shallower Sanibel grounds seems unlikely.

SUMMARY AND CONCLUSIONS

1. In south Florida, mark-recovery experiments with biological stains as the marking agents demonstrated the importance of certain shallow coastal waters as nursery grounds for pink shrimp that eventually frequent the offshore Tortugas and Sanibel grounds.
2. Some shrimp from shallow coastal waters

migrated at least 150 miles before recovery on the offshore grounds.

3. The recovery patterns show that shrimp disperse considerably between release and recovery, suggesting broad migration routes. Despite such dispersion, shrimp emanating from each nursery area indicated a distinct pattern of distribution on the offshore grounds.

4. Shrimp leaving the estuaries and moving across the offshore grounds tend to move into deeper water. Although limited movement into shallower water was noted on the offshore grounds, such movement is apparently only temporary, because recoveries after long free periods were almost always from deeper water.

5. Mark-recovery data reveal that the length of time spent in the estuaries by shrimp may vary from about 2 to at least 6 months.

6. Between release in an estuary and recovery on an offshore trawling ground the minimum free time of any marked shrimp was 35 days, the maximum 331 days.

7. Shrimp available for capture on the Tortugas trawling grounds emanate from shallower waters to the north, northeast, and east of the grounds. In these directions, the Tortugas stock recruitment range extends at least as far as the south Sanibel grounds, Indian Key, Shark River, Flamingo, Bottle Key, Peterson Keys, and that portion of Hawk Channel south of Bahia Honda Key. Thus, a large portion of the estuarine nursery grounds is located within Everglades National Park. Shallows within the Tortugas grounds may also be a source of recruits to this fishery. The affinity to the Tortugas stocks of pink shrimp occurring in deep water east and south of the Florida Keys, and south, west, and northwest of the Tortugas grounds has not been established.

8. Shrimp available for capture on the south Sanibel trawling grounds emanate from shallower waters along the adjacent coast. Coastally, minimum limits of the recruitment area range from Pine Island Sound, to the north, to Indian Key, southeast of the grounds. Offshore, pink shrimp of the south Sanibel stocks occur on the northwest Sanibel grounds and on the northwestern portion of the Tortugas grounds. The relationship of the south Sanibel pink shrimp to those inhabiting deeper water west of the grounds is not known.

9. The Sanibel and Tortugas stocks overlap along the southwest coast of Florida and in the offshore water between the two trawling grounds. There is evidence that young shrimp recruited from nursery grounds as remote as northeastern Florida Bay and Pine Island Sound associate, as adults, in the area intervening between the Sanibel and Tortugas grounds. Apparently Tortugas shrimp do not migrate to the Sanibel trawling grounds, and south Sanibel shrimp seldom migrate to the Tortugas trawling grounds, or to the northwest Sanibel grounds.

10. The geographic distribution of the Tortugas and Sanibel shrimp stocks as presented here constitutes a minimum range. The absence of fishing effort in certain contiguous regions precluded recoveries and, therefore, identification of these regions as part of the range. In addition, insufficient knowledge of the migrations of larval and postlarval shrimp precludes determination of their origin, which may be beyond the region known to be frequented by the Tortugas and Sanibel shrimp stocks as juveniles and adults.

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TIME OF MIGRATION AND AGE GROUP STRUCTURE OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) SPAWNING POPULATIONS IN THE NAKNEK RIVER SYSTEM, ALASKA[1]

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ABSTRACT

The annual sockeye salmon (*Oncorhynchus nerka*) migration to the Naknek River system, Alaska, was studied to determine to what extent major spawning, populations were segregated by their time of occurrence in the run. The extent of segregation by age in the run and on the spawning grounds was also studied.

Daily tagging on the Naknek River and subsequent tag recovery on the spawning grounds showed that segregation of individual spawning populations by time of occurrence in the Naknek run is limited. There was a more or less complete intermingling of most spawning groups throughout the run; consequently, most spawning grounds derive their fish from all parts of the run and, generally, in proportion to the size of the daily escapement.

Daily escapement age analysis indicated the lack of marked segregation by age in the Naknek run. No seasonal trend in age was apparent in the 1962 Naknek run.

Differences in age characteristics of major spawning ground populations indicated segregation by age on the spawning grounds of the Naknek River system.

It is generally accepted that sockeye salmon (*Oncorhynchus nerka*), when mature, return to the river system of their origin to spawn. This homing tendency was recognized as early as 1738 (Krasheninnkov, 1754) and given formal expression as the "home-stream" theory in the early 1900's (Chamberlain, 1907). Over a period of many years, evidence in support of this theory was obtained from marking experiments in various river systems from Oregon to Alaska.

The applicability of the "home-stream" theory to individual spawning areas within a river system was first suggested by Gilbert (1914–16, 1918–20) in his investigation of the sockeye salmon of the Fraser River in British Columbia. He found widely differing scale types on fish from different parts of the Fraser River system. Several areas were characterized by spawning populations having scale types so radically different as to permit conclusive segregation of one spawning population from another. Gilbert concluded that the appearance in the fishery of fish with the different scale types could be used to ascertain changes in the racial composition of the catch. Since Gilbert's early work, timing and duration of abundance of various spawning groups have been established by tagging experiments (Thompson, 1945; Killick, 1955), and racial identification has been determined by scale studies (Clutter and Whitesel, 1956; Henry, 1961).

Studies on the Fraser River and several other major sockeye salmon systems in North America have shown that individual spawning populations tend to be segregated in their time of occurrence in the run. Each population appears to have its own specific requirements for survival that govern the time at which it migrates from the sea. For a number of river systems this time seems to

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Note.—Approved for publication Oct. 7, 1964.

[1] Based in part on a thesis submitted to the graduate school of the University of Hawaii, Honolulu, in partial fulfillment of the requirements for the degree of Master of Science in Zoology, June 1963.

be related to the distance fish must travel to reach the spawning ground and to the type of spawning area they use. In general, it seems that sockeye salmon with the greatest distances to travel occur in the early part of the run, while those with the shortest distances occur in the late part. This is quite evident on the Fraser River and is reported to occur also on the Copper River in central Alaska.[2]

Segregation of spawning groups in time by the type of spawning area utilized has been reported in some systems.

Barnaby (1944) found that fish occurring early in the run populate all the spawning streams entering Karluk Lake on Kodiak Island, whereas most of those appearing late in the run use only the larger streams and lake beaches. Tagging studies on the Skeena River in British Columbia (Fisheries Research Board of Canada, 1957) indicate that sockeye salmon bound for the smaller tributary streams of Babine Lake pass through the fishery earlier than those bound for the outlet spawning grounds.

Seasonal timing may also be related to the age of fish. Rounsefell (1958) presents evidence that "the age of downstream migration has a negative effect on the season of return. The 2-year migrants run first, followed by the 3-, 4-, and finally the 5-year migrants.[3] The ocean age, on the contrary, has a positive effect. The 4-ocean fish run earliest, followed in succession by the 3-, 1-, and 0-ocean fish groups."[4] Similar changes in age composition during the run were reported for the Copper River by Thompson.

Segregation of age groups of sockeye salmon by lake system and by spawning grounds within a lake system has also been reported in the literature. Although the 4_2 age group[5] dominates the Fraser River run annually, three races—the Chilko, Taseko, and Birkenhead—are characterized by a consistent contribution of the 5_3 age group or "2-year-in-the-lake" fish (Henry, 1961). Koo and Smith (1960) noted that various localities in the Iliamna-Clark system of the Kvichak River drainage in Bristol Bay (fig. 1) showed different age compositions. They stated that this was clear evidence of the segregation of subpopulations. Segregation of spawning groups in time and by age might also occur in the commercially important sockeye salmon runs of other river systems of Bristol Bay.

Knowledge of segregation is basic to understanding the dynamics of sockeye salmon stocks. Further, it would provide information essential in designing studies to identify and determine the abundance of populations in the fishery or in the trunk stream before they disperse to the spawning grounds. Finally, such knowledge would have application in showing whether, and to what extent, individual spawning populations could be managed independently in the fishery and what effect present and contemplated regulatory policies could have on these populations.

The purposes of this study were: (1) To determine the extent that major spawning populations of Naknek sockeye salmon may be segregated by time of occurrence in the run, (2) to determine by age study the seasonal pattern of age distribution, and (3) to determine age segregation on the spawning grounds.

The Naknek River system is one of the major producers of sockeye salmon in Bristol Bay (fig. 1). In some years the sockeye salmon run to the Naknek system has exceeded that to the Kvichak River system, which is generally the most pro-

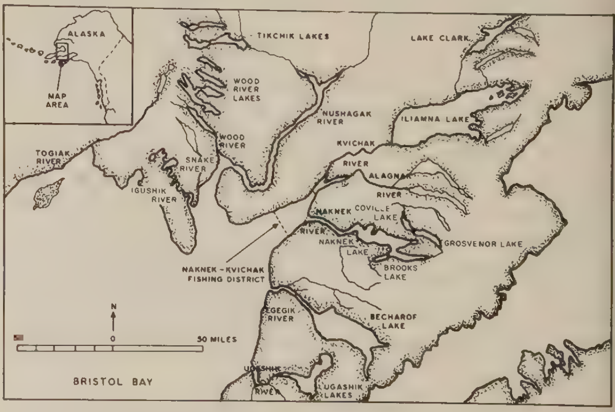

FIGURE 1.—Bristol Bay, showing locations of principal river systems and the Naknek-Kvichak fishing district.

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[2] Thompson, Seton H. The red salmon (*Oncorhynchus nerka*) of Copper River, Alaska. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. (Manuscript).

[3] Refers to the age (figured from time of deposition of the egg) at which the juvenile salmon migrates from fresh water to the sea. Thus, a 2-year migrant is a fish that migrates to sea in its second year of life, a 3-year migrant in its third year.

[4] Refers to the number of winters spent in the ocean before the fish returns to fresh water to spawn.

[5] This method of designating the age of Pacific salmon was first introduced by Gilbert and Rich (1927). The first number denotes the total age of the fish (figured from time of egg deposition), and the subscript represents the year of life that it migrated from fresh water to the sea. Thus, a 4_2 salmon, called "four-two," refers to a fish that migrated to sea in its second year and returned as an adult in its fourth year of life.

ductive, and has made up most of the Naknek-Kvichak commercial catch. The true size of the Naknek run in any one year is difficult to assess because that portion of the run taken in the commercial fishery intermingles in the Naknek-Kvichak fishing district (fig. 1) with sockeye salmon bound for several of the other rivers entering Bristol Bay. In most years the total catch of sockeye salmon in this district has equaled or exceeded the total spawning escapement to these rivers. Spawning escapements in excess of 2 million have been estimated for the Naknek in recent years, giving some indication of the productivity of this system.

Commercial fishing for sockeye salmon in Bristol Bay is done almost entirely by a gill net fishery which is intense and efficient and capable of taking most of the fish in a district during an open fishing period, essentially eliminating spawning escapement. In the present management of the Naknek stocks the entire run is treated as a homogeneous mixture; therefore, to allow spawning escapement from all parts of the run, the fishery is regulated by periodically opening and closing the Naknek-Kvichak district to fishing.

The spawning grounds of the Naknek River system include a complex of four lakes, Naknek, Brooks, Grosvenor, and Coville, and interconnecting and tributary streams (fig. 2). The annual sockeye salmon migration to the Naknek includes fish destined for interconnecting streams, the tributary stream, and beach spawning areas of all four lakes. Before this study, it was not known if spawning groups could be identified by time of migration.

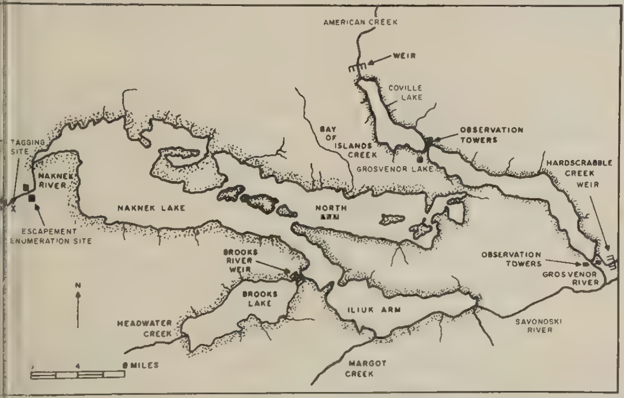

Figure 2.—Naknek River system, showing the location of tagging site, weirs, and observation towers.

The Naknek run is of relatively short duration, normally occurring between mid-June and late July, however, spawning takes place over a considerably longer period of time. Depending on the area utilized, spawning may begin as early as late July or as late as early October. The peaks of spawning activity occur about mid-August on the lake tributary streams and during the latter part of September on the interconnecting streams and lake beaches.

Segregation of populations by age groups by time of occurrence in the run and on the spawning grounds has been reported to occur in other river systems, but before this study, little was known of the extent to which this occurred in the Naknek River system.

MATERIALS AND METHODS

Of the various methods now used to identify races of salmon, the tag and recovery technique supplemented by age analysis was considered to be the most direct means for accomplishing the purposes of this study.

TAGGING OPERATIONS

Salmon were captured and tagged daily in 1962 by Bureau of Commercial Fisheries personnel at a site on the south bank of the Naknek River 24 miles above the mouth (fig. 2). Most of the upstream migration in the vicinity of the tagging site occurs along the south bank of the river.

Sockeye salmon ascending the trunk streams characteristically migrate in a narrow band close to shore. Specimens for tagging were caught in a "seine trap" (fig. 3), consisting of a 400- by 12-foot beach seine having 3-inch mesh (stretch measure). The seine was set by boat from shore and attached to a steel stake driven into the river bottom 150 feet offshore. The remaining 250 feet of seine was allowed to trail downstream with the current, forming a partial rectangular enclosure of about 38,000 square feet open on the downstream side. The free end of the net was attached to shore by a rope. The upstream portion of the seine attached to the stake was fitted with a trip lever that could be released by a rope leading to shore. When an observer located in a tower on the river bank saw fish entering the enclosure, the lever was tripped, releasing the net from the stake and allowing it to be carried downstream around the fish. Meanwhile, the free downstream

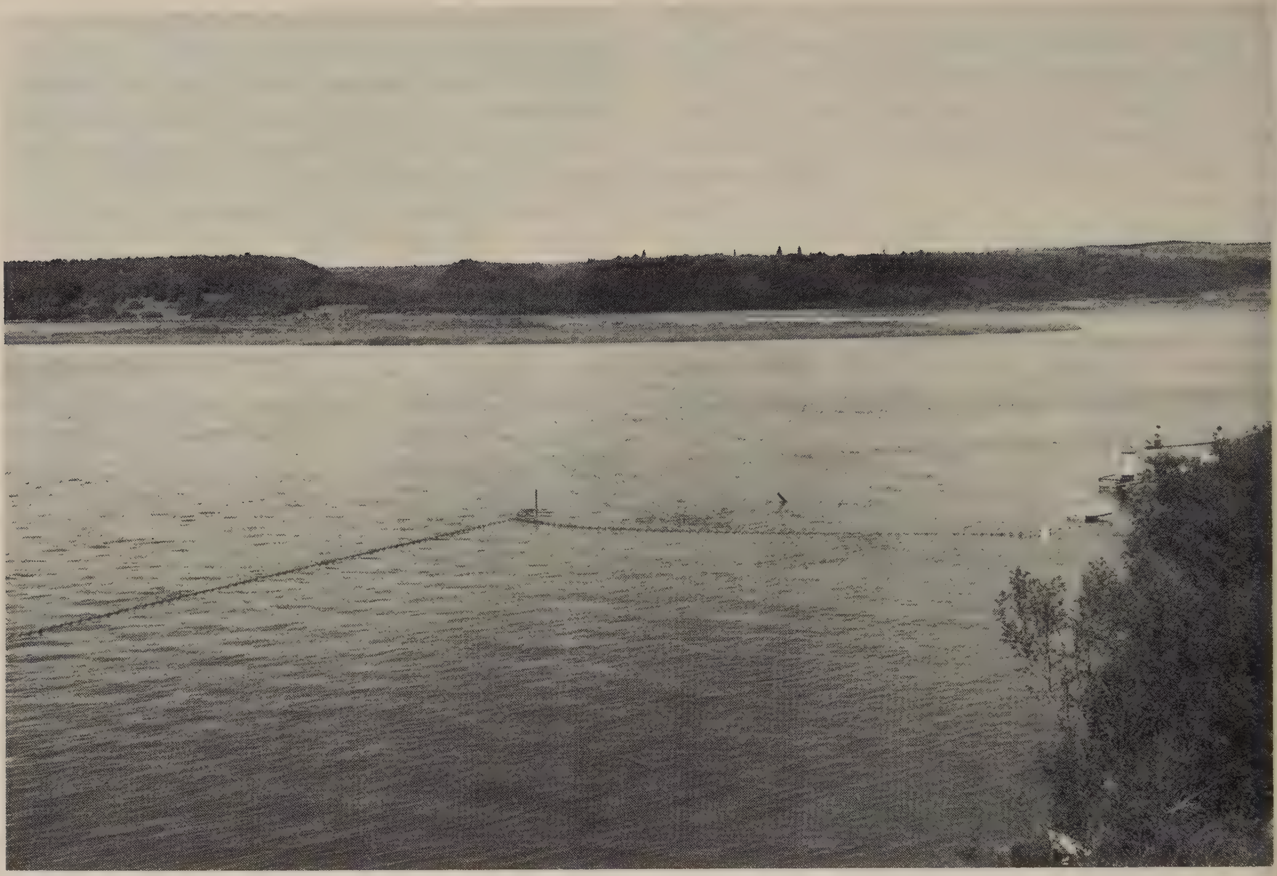

FIGURE 3.—Beach seine trap used to capture sockeye salmon for tagging, Naknek River, 1962. Dock is at right.

end of the net was pulled to shore, completely enclosing the fish.

Three men tagged the fish. The first dipped fish from the holding pen and transferred them to tubs containing an anesthetic; the second transferred the anesthetized fish to the tagging cradle and held it; and the third attached the tag and released the fish.

Two anesthetics were used. From June 24 to 30, tricaine methanesulfonate (MS 222) was used; from July 1 to 18, the remaining period of the experiment, quinaldine was used because of its more rapid action in producing anesthesia.

A pair of 1-inch plastic disk tags was attached to the fish (one on each side) with a nickel pin that was inserted through the fleshy part of the back about 1 inch below the base of the posterior to the insertion of the dorsal fin. A different color combination of tags was used each day (table 1), making it possible to determine the date of tagging through visual observation of tagged fish on the spawning grounds. The tags applied to the left side of the fish were serially numbered.

Between June 24 and July 18, 1962, 6,822 sockeye salmon were tagged (table 1), accounting for 0.94 percent of the estimated total run and giving an estimated tagged to untagged ratio of 1:106.

TAG RECOVERY

Tagged fish recoveries were in the form of both visual observations and actual recaptures. Observations provided information only on the date of tagging. Recaptures yielded additional information on age, length, and sex.

SAMPLING FOR AGE, SIZE, AND SEX

A portion of the fish captured and tagged each day was sampled to determine the age, size, and sex composition of the Naknek spawning escapement. Some fish from every seine haul were sampled, the exact number depending on the size

TABLE 1.—*Sockeye salmon in daily escapements and number and percent tagged, Naknek River, June 24 to July 21, 1962*

Date	Fish in daily escapement[1]	Tag color combination[2]	Fish tagged in daily escapement	
	Number		*Number*	*Percent*
June 24	0	B-G	2	(3)
25	6	W-Y	85	(3)
26	7,122	R-B	31	0.44
27	1,578	G-W	113	7.16
28	1,434	Y-R	6	0.42
29	10,974	B-W	324	2.95
30	74,286	R-G	726	0.98
July 1	20,214	Y-B	109	.54
2	10,956	W-R	144	1.31
3	20,112	G-Y	588	2.92
4	21,666	B-B	525	2.42
5	293,712	R-R	1,704	0.58
6	128,514	Y-W	713	.55
7	115,938	G-G	660	.57
8	6,024	B-Y	178	2.95
9	2,412	W-G	314	13.02
10	1,116	Y-Y	204	18.28
11	1,182	B-R	213	18.02
12	1,194	G-B	106	8.88
13	2,142	R-W	31	1.45
14	954	W-B	25	2.62
15	666	Y-G	11	1.65
16	792	------	0	------
17	372	------	0	------
18[4]	216	R-Y	10	4.63
19	18	------	------	------
20	42	------	------	------
21	24	------	------	------
Total	723,666	------	6,822	0.94

[1] Escapement estimates provided by Alaska Department of Fish and Game. Margin of error determined from previous studies is 3 percent of estimated total run.

[2] Colors used were blue (B), green (G), red (R), white (W), and yellow (Y). The first letter of a color combination designates the left side tag color.

[3] Percent of daily escapement tagged was not completed for the first 2 days. The earliest fish to arrive commonly held up between the tagging and tower sites below the rapids for a day or two until the schools build up in size.

[4] Tagging ended on this date.

of the catch and the magnitude of the daily escapement. If the escapement and seine catch were small, every fish was sampled; if they were large, every second, third, or fourth fish was sampled. A total of 3,094 fish, or about 45 percent of the total number tagged, were sampled.

Samples were also taken from individual spawning grounds during the period of spawning activity and from the weirs on Brooks River and American and Hardscrabble Creeks almost daily. In addition, fish obtained during beach seining for tag recovery records were sampled for age, size, and sex. Survey crews covering the smaller tributary streams for tags sampled the spawners in these areas.

Tagged fish were seen near the outlets of all lakes and on some spawning grounds. Observers in towers located on each bank of the river at the outlet of Grosvenor and Coville Lakes (fig. 2) recorded the number of fish and the color combination of all tags seen entering these lakes. At Brooks Lake observers recorded tagged fish as they passed through counting gates of the Brooks River weir (fig. 2). On certain spawning grounds it was necessary to rely largely on observations of tagged fish, because sometimes the fish could not be recaptured. This was particularly true for salmon spawning on Grosvenor Lake beaches and deep swift portions of Grosvenor River and Naknek Lake outlet areas. Here observers counted tagged fish from towers located on boats.

Actual recaptures of tagged fish were obtained from several sources. On Brooks River and American and Hardscrabble Creeks (fig. 2), tagged fish were obtained at weir traps. Tributary and interconnecting streams that were not checked by means of weirs were surveyed for tagged fish on foot or by boat several times during the spawning period. In some of the larger and deeper streams, tagged fish were recaptured by beach seining or by spearing with the use of skin diving and scuba diving techniques.

Total spawning ground recoveries amounted to 1,202 fish, or about 18 percent of those tagged (table 2). An additional 82 tagged fish were sighted, but the color combinations could not be positively identified.

Scales taken from sockeye salmon at the time of spawning have margins that are absorbed to such an extent that only fresh-water age is discernible on a projector. It was necessary to resort to length-frequency distributions of 2- and 3-ocean sockeye salmon derived from fish sampled at the tagging site (1,428 males and 1,621 females) for the assignment of ocean age to each fish sampled on the spawning ground. Approximately 98 percent of the fish in the 1962 escapement spent 2 or 3 years in the ocean. For assignment of ocean age, the dividing line used between fish of 2-ocean and 3-ocean age was 540 mm. for females and 553 mm. for males. Fish shorter than those lengths were considered as 2-ocean, and those longer as 3-ocean. I found no discrepancies between ages assigned to tagged salmon sampled twice—in the trunk stream and on the spawning grounds.

Fish were measured to the nearest millimeter from the center of the eye to the fork of the tail.

The sex of each fish was determined from external characteristics.

METHODS OF ANALYSIS

Seasonal Timing of Spawning Populations

The extent of segregation of individual spawning populations by time of occurrence in the run may

TABLE 2.—*Numbers of tags recovered on spawning grounds—by color combination, date of tagging, and location—Naknek River system, 1962*

Location	Tag color combination [1] and number of salmon tagged (in parentheses)																							Total
	B-G (2)	W-Y (85)	R-B (31)	G-W (113)	Y-R (6)	B-W (324)	R-G (726)	Y-B (109)	W-R (144)	G-Y (588)	B-B (525)	R-R (1,704)	Y-W (713)	G-G (660)	B-Y (178)	W-G (314)	Y-Y (204)	B-R (213)	G-B (106)	R-W (31)	W-B (25)	Y-G (11)	R-Y (10)	
	June							July																
	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18	
Naknek Lake:																								
Naknek River lake outlet		2	1			6			3		7	18	7	2	2		3		2		3	2		58
Bay of Islands Creek						1			3	1	3	17	4	1	2	1	5	1	1					40
Margot Creek						4	2	1	1	7	5	22	3	6		2	2	3	1				2	61
Brooks River		1		3		12	8	5	12	21	30	59	29	17	8	5	11	13	11	4	1			250
Grouped lateral streams		2	1				3		2	5	7	12	6	1		1	3	4		1				48
Iliuk Arm Beach												1	1											2
Miscellaneous [2]		1										1	1	1	1									5
Brooks Lake:																								
Grouped lateral streams [3]			[1]		[1]	[3]	[2]		[2]	[2]		[5]	[6]		[1]		[3]							[26]
Headwater Creek [3]									[2]			[1]	[2]			[1]						[1]		[7]
Weir count [4]		1	4	4	1	13	20	2	4	12	9	33	25	9	4	4	3	2			2	1	1	154
Savonoski River:																								
Dick's Creek							1		1	6		5	1		1									15
Grosvenor Lake:																								
Grosvenor-Coville connecting stream				1															1					2
Grouped lateral streams				1		1	1	2	1	3	4	6	5	4	1	3	1	1	1					35
Hardscrabble Creek		2		2		2	8		10	10	20	29	16	7	1	4	5	5	2	1				124
Grosvenor River										2	4	9	7	3		1	1	2	1	1			1	32
Beach spawning area											2	6	2				2							12
Coville Lake:																								
American Creek			1	4		11	14	3	10	34	47	94	57	24	5	18	16	12	3	1	2		4	360
Grouped lateral streams												2	2											4
Total		9	7	15	1	50	57	13	47	101	138	314	166	75	25	39	52	43	23	8	8	3	8	1,202

[1] Colors used were blue (B), green (G), red (R), white (W), and yellow (Y). The first letter of a color combination designates the left side tag color.
[2] Location of recovery unknown.
[3] The figures in this entry are placed in brackets because they are included in the Brooks Lake weir counts and have therefore been excluded from the total at the bottom of the column.
[4] Corrected upstream count taken as lake total.

be shown by the number and distribution of color combinations of tagged fish on the spawning grounds. Theoretically, with no segregation the frequency distributions of color combinations occurring on particular spawning grounds should be similar to those of the overall tagged population.

Because of the size and depth of many spawning areas we could not recapture or see all tagged fish present. If the likelihood of recapture or observation were equal for all tag color combinations, spawning ground recoveries should have reflected the relative proportion of tags from each day of tagging. Minor disagreement between actual and expected tag recovery proportions could have occurred as a result of sampling variation and would not necessarily indicate segregation. On the other hand, any substantial disagreement could be taken as a sign of segregation.

Actual tag recoveries were compared with the expected recoveries for major spawning grounds of the Naknek system in two ways: (1) By graphical comparison of the pattern of weighted spawning ground recoveries by day of tagging with the pattern of the daily escapement passing the tagging site, and (2) by statistical comparison using contingency χ^2 analysis (Snedecor, 1956) to test the hypothesis of like tag recovery distributions between spawning areas.

It would have been desirable to tag a given proportion of the run each day so that individual spawning populations would have been tagged in proportion to their daily abundance. This would have made it possible to compare directly the spawning ground recoveries for each day of tagging with the appropriate daily escapement size. This could not be done, however, because the size of the daily escapement, which was counted upstream from the tagging site, was unknown before each day's tagging.[6] Salmon in the escapement were counted daily from observation towers located on each bank of the river 1½ miles upstream from the tagging site (fig. 2). Counting migrating sockeye salmon from towers has been proved a reliable method of assessing the size of daily escapements in Bristol Bay[7] (Becker, 1962).

The number of recoveries was dependent on the number of fish tagged ($r-0.949$, d.f.$=21$, $P\,(0.001)$), but because a different proportion of the run was tagged each day, recoveries were weighted to make them directly comparable to the daily escapement size. Weighting was accomplished by adjusting the number of fish tagged each day to a standard proportion of the daily escapement. The standard selected was the proportion tagged (0.58 percent) on July 5, the day when the greatest number of fish were tagged (table 1). Weighted spawning ground recoveries for each day's tagging were obtained as follows:

$$W=\frac{0.58A}{X}$$

Where:

W=Weighted recoveries
A=Actual recoveries
0.58=Proportion of the escapement tagged on day of greatest tagging
X=Proportion of the run tagged on day in question

For any spawning area, the proportion of adjusted recoveries for each day of tagging is thus directly comparable to the daily escapement. I obtained the graphical pattern of tag recoveries for selected spawning areas by plotting the percentage of the total adjusted recoveries by day of tagging and compared this pattern with that of the daily escapement, which was obtained by plotting the percentage of the total escapement on each day of tagging. The amount of disagreement or similarity between the two graphs indicated the extent of segregation.

We recovered adequate tags to make this comparison for most of the known major spawning grounds of the Naknek system; however, for some areas the difficulty encountered in sampling the spawning populations resulted in insufficient recoveries to make comparisons. These included the beach spawning areas of Grosvenor Lake, the tributary streams of the Savonoski River, and a "suspected" beach spawning area in Iliuk Arm of Naknek Lake (fig. 2). For most of the small lateral tributary streams with small spawning escapements, tag recoveries were so few that streams had to be grouped to provide sufficient recoveries for comparison.

Some problems were encountered in identifying tag color combinations. In shallow-water streams

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[6] Estimates of the daily escapement size were provided by the Alaska Department of Fish and Game (table 1).

[7] Staff of the Administration of Alaska Commercial Fisheries. 1956. Progress report and recommendations for 1957, 34 pp. [Processed.]

(less than 5 feet deep), most tag color combinations were easily identified, but in deep-water spawning areas (more than 5 feet deep), most observers reported some difficulty in positively identifying green tags and in distinguishing light blue and yellow tags from white. Red tags were identified the most easily in deep water. Thus, the assumption of equal likelihood of observation for all tag color combinations would not hold true for fish in deep water. The degree of efficiency of observing tagged fish in deep water depends on the depth of the water and the tag color combination. Fortunately, most known spawning in the Naknek system takes place in water that is less than 5 feet deep.

In analyzing recoveries for the experiment, I compared the following spawning areas and the escapement in the manner described above.

1. Individual lakes, i.e., Naknek, Brooks, Grosvenor, and Coville. In this comparison the corrected upstream Brooks River weir count of tagged fish was used as the total recoveries for the lake. This was done because few tags were returned from the Brooks Lake tributary streams. The upstream tag count was corrected by deducting tagged fish that moved back downstream through the weir to spawn in Brooks River. For the other lakes, tag recaptures and sightings obtained by all methods (i.e., during stream surveys, at spawning stream weirs, by beach seining, and by skin diving) were totaled for all streams draining into each lake.
2. Individual, large major valley or terminal streams with similar physical characteristics and periods of spawning activity and with recorded escapements in excess of 10,000 fish. These include American, Hardscrabble, Margot, and Bay of Islands Creeks which drain into Coville, Grosvenor, and Naknek Lakes respectively (fig. 2). Headwater Creek, major tributary of Brooks Lake, had too few recoveries for comparison (table 2).
3. Interconnecting streams (Brooks and Grosvenor Rivers).
4. Grouped small lateral tributary streams of all four lakes combined.
5. Naknek River area at the outlet of Naknek Lake.

Recoveries for days or periods of tagging were arranged in contingency tables for comparisons between selected spawning areas, and the proportion of tags in each period was teste
independence by chi-square. Spawning
compared in this manner were essentially
listed above. In addition, tag recoveries
the small lateral streams of each lake were gro
to provide adequate numbers for testing and
treated as a single spawning unit. Tag reco
proportions for lateral streams of each lake
compared and tested. Comparisons and
were also made between spawning areas of u
physical characteristics, escapement records,
spawning periods (i.e., between the large m
valley streams, small lateral streams, and i
connecting streams).

For most of the areas compared, tag recove
from single days of tagging were too few to per
tests of independence on a day-to-day ba
and sufficient recoveries were obtained by co
bining the recoveries from several continu
days of tagging into a number of periods t
included all 23 days of tagging. Tests of in
pendence were thus made on a period-to-per
basis.

Tests for segregation were grouped into taggi
periods based on the area of spawning. In t
lakes, the 23-day tagging experiment was divid
into seven tagging periods with 3 days in ea
period, except the first and last periods, whi
had 4 days. In the other spawning areas, it w
necessary to group the taggings into three perioc
These periods were unequal in length because th
were based on the daily escapement pattern
the run (table 1). The first period, representi
early-run salmon, included recoveries from taggin
between June 24 and July 2. This period co
tained an early peak of abundance, which is usuall
characteristic of the Naknek sockeye salmon ru
This early peak may represent spawning group
that are segregated in time of occurrence an
destined for particular spawning areas. Th
second period representing middle-run fish, whic
compose most of the escapement, extended fro
July 3 to 8, inclusive. The third period, repre
senting "tail-of-the-run" fish, included recoverie
from July 9 to 18 taggings.

Age Segregation by Time of Occurrence on the Ru and on the Spawning Grounds

Segregation of population by age groups by time o
occurrence in the run was studied as follows. Th
percentages of the various age groups in the dail

escapement were determined from scale readings. Percentages for the four dominant age groups (4_2, 5_2, 5_3, and 6_3), which made up 98 percent of the 1962 escapement, were plotted graphically for each day of sampling. This was done for males and females, both separated and combined. The graphs were examined to determine if particular age groups tended to be segregated in certain portions of the run. Similar graphs were prepared for the percentage of salmon that had spent 2 and 3 years in fresh water and 2 and 3 years in the ocean. The 1962 escapement was composed almost entirely (99.8 percent) of fish of 2- and 3-fresh-water age, and 98 percent of 2- and 3-ocean age. These graphs were examined for the extent of segregation by both fresh-water and ocean ages.

Age segregation on the spawning grounds was studied by comparing the age composition of individual spawning ground samples with each other and with age composition of the total escapement. The age composition of the total escapement was derived from the daily percentage age composition, weighted according to the size of the daily escapement. The escapement and spawning ground age compositions were compared on the basis of age group and of fresh-water and ocean ages. Theoretically, with representative sampling of all spawning areas, a lack of segregation by age categories would be shown by close agreement between the total escapement and the individual spawning ground age compositions. Substantial disagreement would indicate segregation.

The frequencies of occurrence of the four age groups (i.e., 4_2, 5_2, 5_3, 6_3) in most of the run were arranged in a contingency table to compare the age compositions of the individual major spawning grounds of the Naknek system. The proportion of fish in each age group was then tested for independence by chi-square. A probability value of less than $P=0.01$ was considered to indicate unlike age compositions between the areas tested and, therefore, segregation by age on the spawning grounds.

RESULTS AND DISCUSSION

Extent of Segregation by Time of Occurrence in the Run

Graphical comparisons of the pattern of weighted recoveries by day of tagging with the pattern of the daily escapement are a somewhat subjective approach to studying the extent of segregation. On the other hand, statistical tests of like tag recovery distributions between spawning areas are objective in nature. Results obtained by both methods were similar.

Results of Graphical Comparisons

Graphical comparisons of the pattern of weighted tag recoveries for individual spawning areas by days of tagging with the pattern of daily escapement to the entire system are presented in figures 4–7.

It is obvious from these comparisons that most of the spawning areas derive their escapement from all portions of the run. In most areas the proportion of tag recoveries appears, in general, to be related to the size of the escapement on the date of tagging. Greater variability between the tag recovery and escapement pattern is apparent for such areas as Bay of Islands and Margot Creeks, Grosvenor River, and Naknek River at

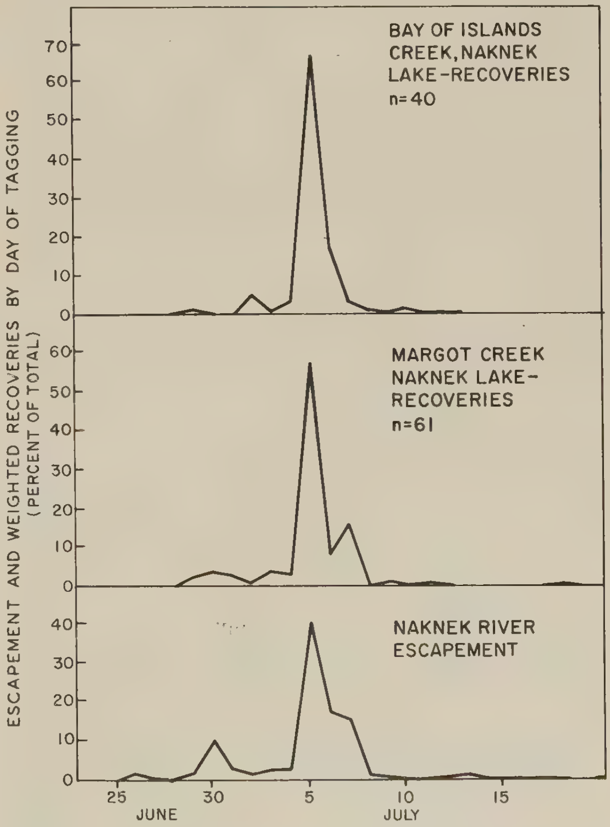

FIGURE 4.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (Margot and Bay of Islands Creeks).

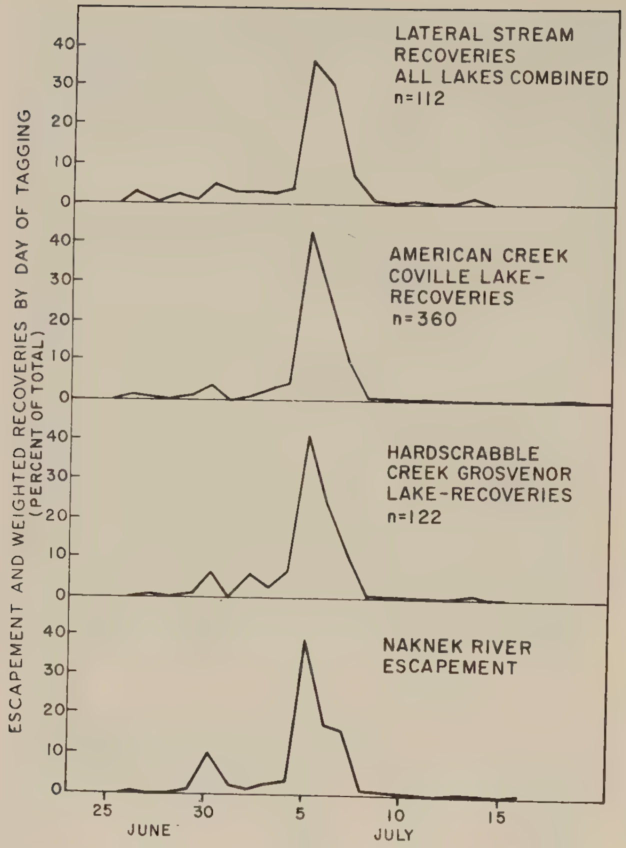

FIGURE 5.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (lateral streams, American Creek, and Hardscrabble Creek).

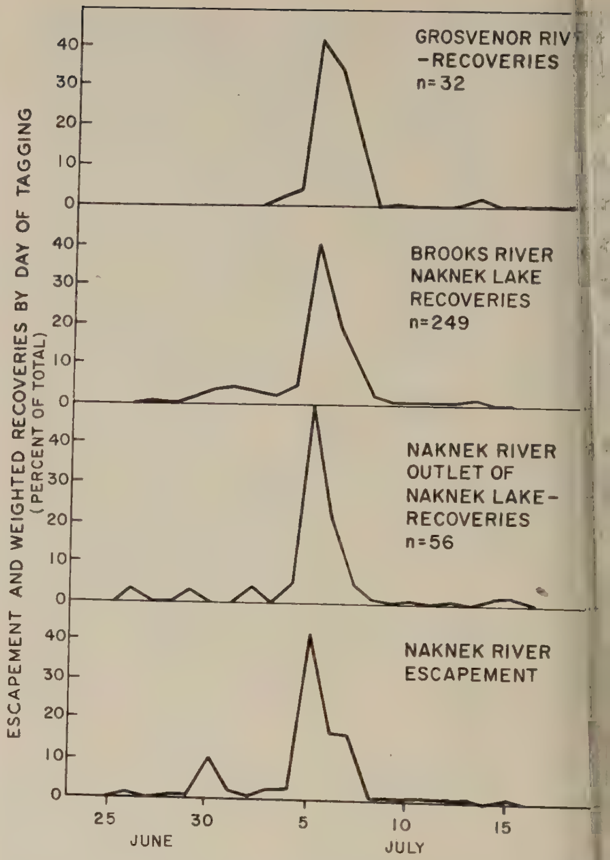

FIGURE 6.—Naknek River escapement and weight spawning ground tag recovery distributions by day tagging, 1962 (Naknek River, Brooks River, ar Grosvenor River).

the outlet of Naknek Lake (figs. 4 and 6), which had a small number of recoveries (table 2). Spawning areas such as American Creek and Brooks River (figs. 5 and 6), which had a substantial number of recoveries, tend to conform more closely to the daily escapement pattern.

The tag recovery pattern for American Creek (fig. 5) is taken to be representative of the entire escapement into Coville Lake. American Creek, one of the most important spawning areas in the Naknek system, usually receives practically the entire spawning escapement entering Coville Lake. The escapement to the few small lateral streams of Coville Lake in 1962 was only a fraction of that which spawned in American Creek. Only four tags were recovered from these streams (table 2), and they do not change the pattern illustrated by the American Creek recoveries.

The small lateral streams of all lakes had to few tag recoveries for comparison with the escapement on an individual basis; however, the few tag obtained from individual lateral streams were from tags applied throughout the run. When these recoveries are grouped by lakes and weighted in the manner previously described, they provide a pattern quite similar to that of the escapement (fig 5). The indication is that the escapement to the small lateral streams is also derived from all parts of the run and generally in proportion to the size of the daily escapement.

Two areas, however, seem to show some degree of segregation of their spawning populations. The pattern of recoveries for Brooks Lake shows a greater proportion of tags from the early portion of the run (i.e., before July 2) than the pattern for the other lakes (fig. 7). This is evident not

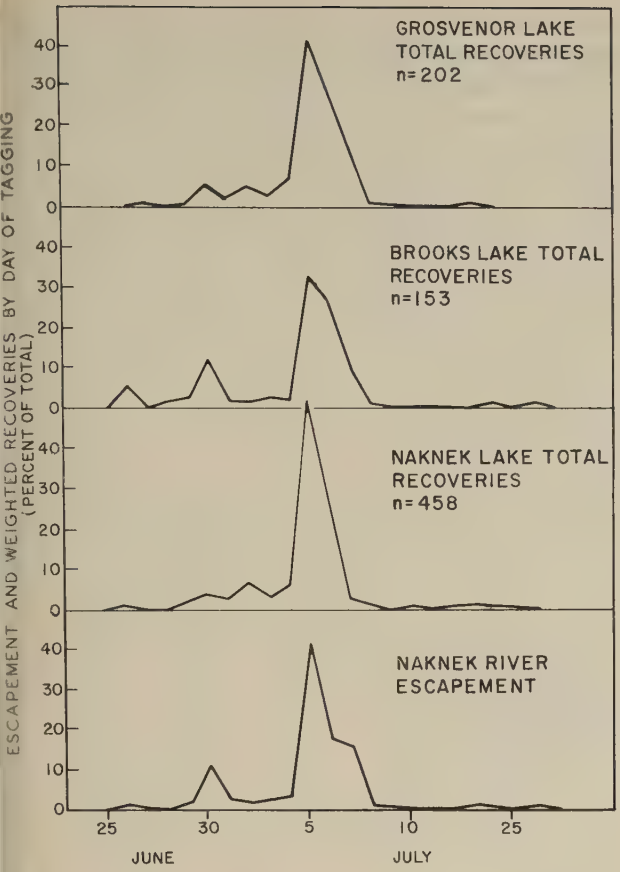

FIGURE 7.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (Grosvenor Lake, Brooks Lake, and Naknek Lake).

only in the Brooks River weir tagged fish count but also in the tag recoveries from the streams tributary to Brooks Lake (table 2).

Grosvenor River had no tagged fish from the early part of the run (fig. 6). Grosvenor River is one of the areas where considerable difficulty was experienced in recapturing tagged fish and in identifying the color combination of those sighted. It is possible, because of the generally smaller numbers of fish tagged in the early part of the run and the few tagged fish recaptured or identified (table 2), that sampling was inadequate and early-run fish were missed as a result of chance. On the other hand, fish from late-run taggings (i.e., after July 2) comparable in size to fish in some early-run taggings were recaptured or sighted in Grosvenor River. This plus the fact that tags were not recovered from the only large tagging day, June 30, in the early part of the run (table 1) strongly suggests segregation of the Grosvenor River population in the latter part of the run. Not enough tags were recovered, however, to formulate a definite conclusion concerning the segregation of the Grosvenor River spawning populations.

Results of Statistical Comparisons

Chi-square tests of the hypothesis of like recovery distributions for comparisons between similar and dissimilar spawning areas yielded results that substantiate those presented above. Probability values less than $P=0.05$ are considered to indicate unlike tag recovery distributions and, therefore, segregation in time of occurrence in the run.

For the comparison between major valley or terminal streams (American, Hardscrabble, Bay of Islands, and Margot Creeks (table 3)), a value of $\chi^2=5.38$, d.f.$=6$, $P=0.50$ was obtained. This high value of P indicates no significant difference between the tag recovery distributions for these streams and, therefore, little segregation of their spawning populations by time of occurrence in the run.

A value of $\chi^2=4.49$, d.f.$=4$, $P=0.37$ was obtained from the comparison of recovery distributions for the grouped lateral streams of Naknek, Brooks, and Grosvenor Lakes (table 4). Coville Lake lateral streams could not be included

TABLE 3.—*Numbers of tags recovered by dates of tagging for major valley streams, Naknek River system, 1962*

Stream	Tags recovered by dates of tagging			Total
	June 24–July 2	July 3–8	July 9–18	
Bay of Islands Creek	4	28	8	40
Margot Creek	8	43	10	61
Hardscrabble Creek	24	83	17	124
American Creek (Coville Lake)	43	261	56	360
Total	79	415	91	585

TABLE 4.—*Numbers of tags recovered by dates of tagging for grouped lateral streams, Naknek River system, 1962*

Lake	Tags recovered by dates of tagging			Total
	June 24–July 2	July 3–8	July 9–18	
Naknek	7	31	9	47
Grosvenor	6	23	6	35
Brooks	9	14	3	26
Total	22	68	18	108

in the comparison because of insufficient tag recoveries. This high value of P indicates a lack of segregation of lateral stream spawning populations by time of occurrence in the run.

The comparison between the total recovery distributions of Naknek, Brooks, Grosvenor, and Coville Lakes (table 5) yielded a P of less than 0.005, suggesting a difference in time occurrence in the run for the populations destined for these lakes. However, almost two-thirds of the chi-square value of 56.57, d.f.=18 is due to the occurrence of a greater than expected proportion of early-run tagged fish in the Brooks Lake escapement (fig. 7). If the Brooks Lake tag recoveries are excluded from consideration and a comparison made only between Naknek, Grosvenor, and Coville Lakes recovery distributions, the resulting $\chi^2=7.43$, d.f.=12, $P=0.82$. Thus, the recovery distributions for these three lakes are not significantly different, and segregation of their spawning populations as a whole is minimal. For Brooks Lake, however, results suggest that it derived a relatively greater proportion of its spawning population from the early part of the run than did the other three lakes.

TABLE 5.—*Numbers of tags recovered by dates of tagging for Naknek, Brooks, Grosvenor, and Coville Lakes, 1962*

Lake	Tags recovered by dates of tagging							Total
	June 24–27	June 28–30	July 1–3	July 4–6	July 7–9	July 10–12	July 13–18	
Naknek	11	36	61	233	50	60	13	464
Brooks	9	34	18	67	17	7	3	155
Grosvenor	5	12	26	110	25	21	3	202
Coville	5	25	47	202	47	35	7	368
Total	30	107	152	612	139	123	26	1, 189

Comparison of the tag recovery distributions of unlike spawning grounds, which include the grouped lateral streams of all lakes, Brooks and Grosvenor Rivers (representing interconnecting streams), and American and Hardscrabble Creeks (representing major valley streams) (table 6), yielded a value of $\chi^2=14.87$, d.f.=8, $P=0.06$. This value is essentially at the level of probability ($P=0.05$) below which values of P are considered to indicate unlike tag recovery distributions. The cause of the large χ^2 and resulting low probability level is associated with the absence of early-run (June 24 to July 2) tagged fish in the Grosvenor River recoveries (fig. 6). More than one-third of the χ^2 value of 14.87 is caused by the lack of t early-run tagged fish. Although, statistically test does not indicate a tag recovery distribu for Grosvenor River unlike that of the o spawning grounds, the lack of early-run tag fish in the recoveries and the resulting large square suggest that this area may have derive escapement primarily from the latter part of run. If Grosvenor River recoveries are exclu from consideration and a comparison made between the grouped lateral streams, Ameri Creek, Brooks River, and Hardscrabble Creek, resulting $\chi^2=8.70$, d.f.=6, $P=0.20$.

TABLE 6.—*Numbers of tags recovered by dates of tagging unlike spawning grounds, Naknek River system, 196*

Spawning ground	Tags recovered by dates of tagging			Tot
	June 24–July 2	July 3–8	July 9–18	
Grouped lateral streams:				
All lakes	22	68	18	
Major valley streams:				
American Creek	43	261	56	
Hardscrabble Creek	24	83	17	
Interconnecting streams:				
Brooks River	41	164	45	
Grosvenor River	0	25	7	
Total	130	601	143	

Discussion

There is some evidence of heterogeneity betwee the individual spawning ground tag recovery di tributions as compared above. Only Brooks Lak had a tag recovery distribution that differed signif cantly from those of the other spawning grounds The distributions for both the lateral streams an the escapement as a whole show that a highe proportion of early-run fish entered Brooks Lak than the other three lakes. Grosvenor River recoveries indicate that it may have received it escapement primarily from the middle and late parts of the run (i.e., after July 2).

Apart from the above situations, however, the evidence presented fails to indicate any clear segregation of most of the known spawning populations composing the Naknek run. It is clear that the recovery distributions for most spawning areas are not significantly different from one another or from the seasonal escapement pattern in the trunk stream. Most areas apparently derive their spawning populations from all parts of the run and, generally, in proportion to the daily escapement.

As mentioned earlier, the Naknek River sockeye salmon run is of relatively short duration when compared with rivers like the Fraser and Karluk. The total spawning escapement enters the Naknek system during a 4- to 6-week period, and normally over half the total escapement occurs in a period of 3 to 5 days (table 1). Spawning activity, however, occurs over a period of 2½ months, although the period and duration of spawning are quite different for the various grounds used. Time of spawning apparently has little effect in producing segregation. Regardless of the characteristics of spawning activity, most grounds seem to receive their escapement proportionately from all parts of the run.

It seems apparent that the short duration of the Naknek run is not an adaptation to a single optimum spawning period for the Naknek system as a whole, and it is probable that the conditions responsible for the compressed nature of the run occur in the ocean before Naknek salmon reach Bristol Bay. Regardless of the cause, it is likely that the short duration of the run is responsible for the significant lack of segregation. The result is, of necessity, a more or less complete intermingling of the spawning populations composing the Naknek sockeye salmon run in the trunk stream and, therefore, in the fishery. In view of this, it seems impossible now to manage in the fishery the individual spawning groups composing the run.

AGE SEGREGATION BY TIME OF OCCURRENCE IN THE RUN

The daily percentages of the four dominant age groups (4_2, 5_2, 5_3, and 6_3) in the 1962 escapement were determined from samples of fish taken at the tagging site. Little difference was noted between the daily age composition of males and females. Both sexes showed similar daily fluctuations in abundance. The age data for males and females were, therefore, combined (fig. 8).

Although daily fluctuations in age composition of the escapement did occur, there were no marked changes in age composition during the run. Only the 5_3 age group appeared to increase in relative abundance toward the end of the run. During the peak escapement period of July 5–7 (table 1), the proportion of the 5_2 age group was somewhat higher and the 5_3 group lower than the overall seasonal average for these groups. Except for daily fluctuations, there appears to be little change in the age composition of the escapement with the passage of time. Segregation on the basis of age groups appears to have been minimal in the 1962 Naknek escapement.

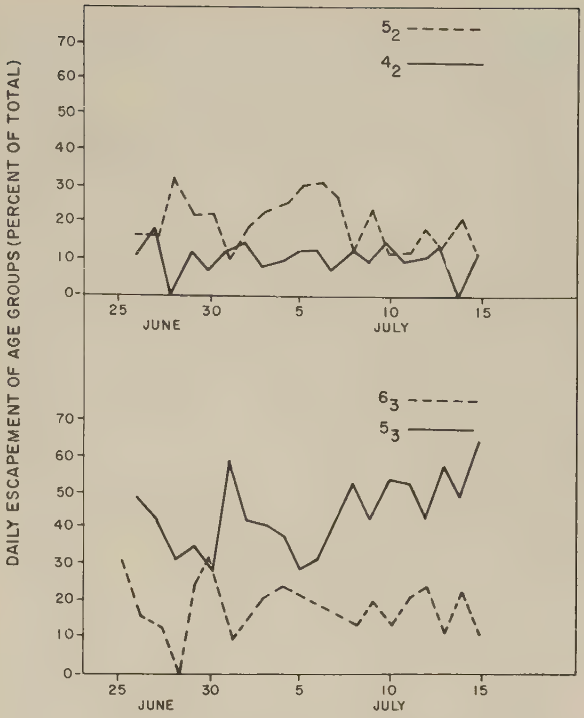

FIGURE 8.—Percent contribution of four dominant age groups of sockeye salmon by day of tagging in Naknek River escapement, 1962.

In figure 9 the daily age composition of the escapement is replotted by fresh-water and ocean age. When examined from this standpoint, only minor changes in age composition appear to occur during the run. The proportion of 3-fresh-water fish increases, while the 2-fresh-water group decreases slightly after the peak escapement period of July 5–7. Also, the proportion of 3-ocean fish is somewhat higher and that of 2-ocean fish lower during the peak escapement period. There is, however, no marked change in the proportion of any age category during the run. Segregation in time by ocean and fresh-water age appears to have been limited in the 1962 escapement.

To what extent the daily age composition of the Naknek escapement is altered by effects of the fishery is unknown. It is known, however, that the Bristol Bay gill net fishery tends to be selective for the larger or 3-ocean fish (i.e., the 5_2 and 6_3 age groups). It is possible that the fishery could account for the marked day-to-day fluctuations

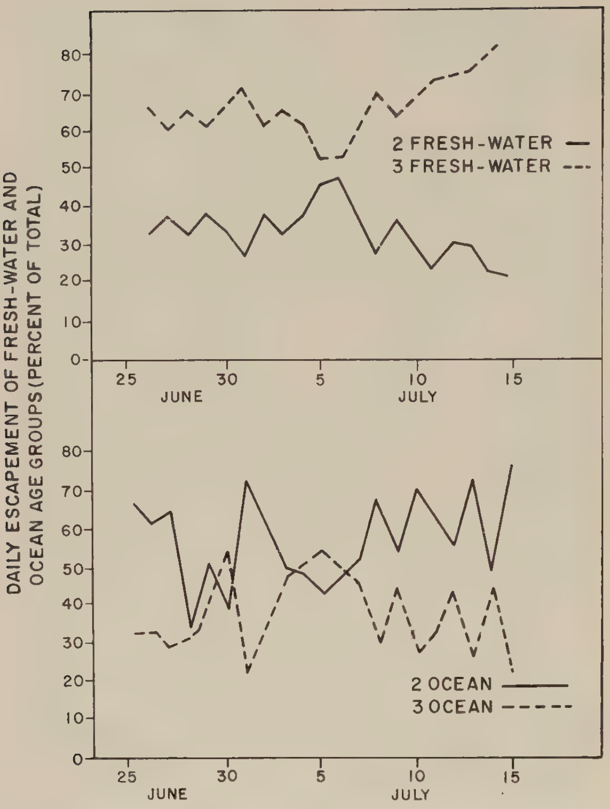

FIGURE 9.—Percent daily age composition of sockeye salmon by fresh-water and ocean age, Naknek River escapement, 1962.

that sometimes occur in the age composition and perhaps produce or mask seasonal trends in age.

AGE SEGREGATION ON THE SPAWNING GROUNDS

Results

In figures 10 and 11 and table 7 the age compositions of fish sampled on the spawning grounds are compared with the age compositions of fish sampled at the Naknek River tagging site. In the figures only the individual spawning grounds of each lake with a sample size greater than 25 are compared with the Naknek River samples. Comparisons are made on the basis of dominant age groups (i.e., 4_2, 5_2, 5_3, and 6_3) and fresh-water and ocean age. A complete summary of all age categories present in the samples obtained from all spawning grounds covered in this study is given in table 7.

Figures 10 and 11 and table 7 reveal marked variation in the age composition of the spawning ground samples when compared with each other and with Naknek River samples. This strongly suggests the segregation of populations by age on the spawning grounds of the Naknek River system.

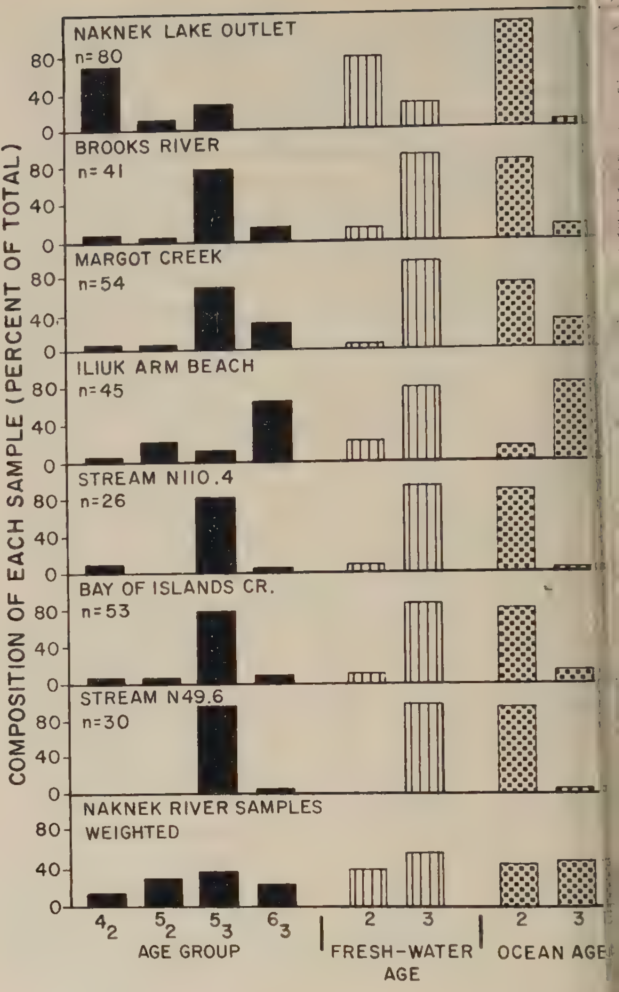

FIGURE 10.—Percent composition of sockeye salmon escapement for major spawning tributaries of Naknek Lake by age group and fresh-water and ocean age, 1962.

For the major spawning grounds of the Naknek system, the frequencies of occurrence of the four dominant age groups are arranged in a 4-by-9 contingency table (table 8). A chi-square test of the hypothesis of like age compositions for the spawning grounds being compared yielded a value of $\chi^2=549.21$, d.f.$=24$, $P=0.005$. Since the value of P is well below the adopted 0.01 level of significance, it constitutes convincing evidence of unlike age compositions between the areas compared and, therefore, segregation by

TABLE 7.—*Age composition of sockeye salmon on spawning grounds by number and percent, Naknek River system, 1962*

Location	Age group											Fresh-water age			Ocean age			
	3_2	4_2	4_3	5_2	5_3	6_2	6_3	6_4	7_3	7_4	Total	2	3	4	1	2	3	4
Naknek Lake:																		
Stream N 16.1:																		
Number		4	1		3		3				11	4	7		1	7	3	
Percent		36.4	9.1		27.3		27.3					36.4	63.6		9.1	63.6	27.3	
Stream N 18.7:																		
Number		2			3			1			6	2	3	1		6		
Percent		33.3			50.0			16.7				33.3	50.0	16.7		100.0		
Stream N 19.6:																		
Number			1		3			1			5		4	1	1	4		
Percent			20.0		60.0			20.0					80.0	20.0	20.0	80.0		
Stream N 23.4:																		
Number		4			5						9	4	5			9		
Percent		44.4			55.6							44.4	55.6			100.0		
Stream N 49.6:																		
Number					29		1				30		30			29	1	
Percent					96.7		3.3						100.0			96.7	3.3	
Stream N 56.4:																		
Number			1		1						2		2		1	1		
Percent			50.0		50.0								100.0		50.0	50.0		
Bay of Islands Creek:																		
Number		3	1	3	41		5				53	6	47		1	44	8	
Percent		5.7	1.9	5.7	77.4		9.4					11.3	88.7		1.7	83.2	15.1	
Stream N 93.7:																		
Number					20		2				22		22			20	2	
Percent					90.9		9.1						100.0			90.9	9.1	
Stream N 110.4:																		
Number		2	2		21		1				26	2	24		2	23	1	
Percent		7.7	7.7		80.8		3.8					7.7	92.3		7.7	88.5	3.8	
Stream N 111.4:																		
Number				1	6		1				8	1	7			6	2	
Percent				12.5	75.0		12.5					12.5	87.5			75.0	25.0	
Stream N 133.3:																		
Number				1	5		3				9	1	8			5	4	
Percent				16.7	55.6		33.3					11.1	88.9			55.6	44.4	
Iliuk Arm Beach:																		
Number		1		9	6		29				45	10	35			7	38	
Percent		2.3		20.0	13.3		64.4					22.2	77.8			15.6	84.4	
Margot Creek:																		
Number		1		2	36		15				54	3	51			37	17	
Percent		1.9		3.7	66.7		27.8					5.6	94.4			68.5	31.5	
Stream N 142.7:																		
Number		1			5						6	1	5			6		
Percent		16.7			83.3							16.7	83.3			100.0		
Brooks River:																		
Number		3	1	1	30		5	1			41	4	36	1	1	34	6	
Percent		7.3	2.4	2.4	73.2		12.2	2.4				9.8	87.8	2.4	2.5	82.9	14.6	

Location	Age group												Fresh-water age			Ocean age			
	3_1	3_2	4_2	4_3	5_2	5_3	6_2	6_3	6_4	7_3	7_4	Total	2	3	4	1	2	3	4
Naknek Lake:																			
StreamN 156.9:																			
Number			1			2						3	1	2			3		
Percent			33.3			66.7							33.3	66.7			100.0		
Stream N 170.3:																			
Number			1			23						24	1	23			24		
Percent			4.2			95.8							4.2	95.8			100.0		
Lake outlet:																			
Number		1	54		5	20						80	60	20		1	74	5	
Percent		1.3	67.5		6.2	25.0							75.0	25.0		1.3	92.5	6.2	
Brooks Lake:																			
Weir samples:																			
Number	2	4	137	19	183	975	7	107	2	2		1,438	331	1,103	2	23	1,116	290	9
Percent	0.1	0.3	9.5	1.3	12.7	67.8	0.5	7.5	0.1	0.1			23.0	76.7	0.14	1.6	77.6	20.2	0.6
Grosvenor Lake:																			
Lateral streams:																			
Number			4		5	19		8				36	9	27			23	13	
Percent			11.1		13.9	52.8		22.2					25.0	75.0			63.9	36.1	
Lake beaches:																			
Number			6		20	8	1	50				85	27	58			14	70	
Percent			7.1		23.5	9.4	1.2	58.8					31.2	68.2			17.6	82.4	
Hardscrabble Creek:																			
Number			17		19	55		53	1		1	146	36	108	2		73	73	
Percent			11.6		13.0	37.7		36.3	0.7		0.7		24.7	74.0	1.3		50.0	50.0	
Grosvenor River:																			
Number			8		8	30		45	1		2	94	16	75	3		39	55	
Percent			8.5		8.5	31.9		47.9	1.06		2.1		17.0	79.8	3.2		41.5	58.5	
Coville Lake:																			
American River:																			
Number			35	1	193	149	1	295	1	1	1	677	230	446	2	2	185	489	2
Percent			5.2	0.15	28.5	22.0	0.15	43.5	0.15	0.15	0.15		33.9	65.8	0.30	0.30	27.3	72.1	0.3
Naknek River samples weighted: percent		0.1	11.9	0.6	28.7	35.7	1.3	21.4		0.2	0.3		41.9	57.8	0.2	0.7	47.6	50.2	1.5

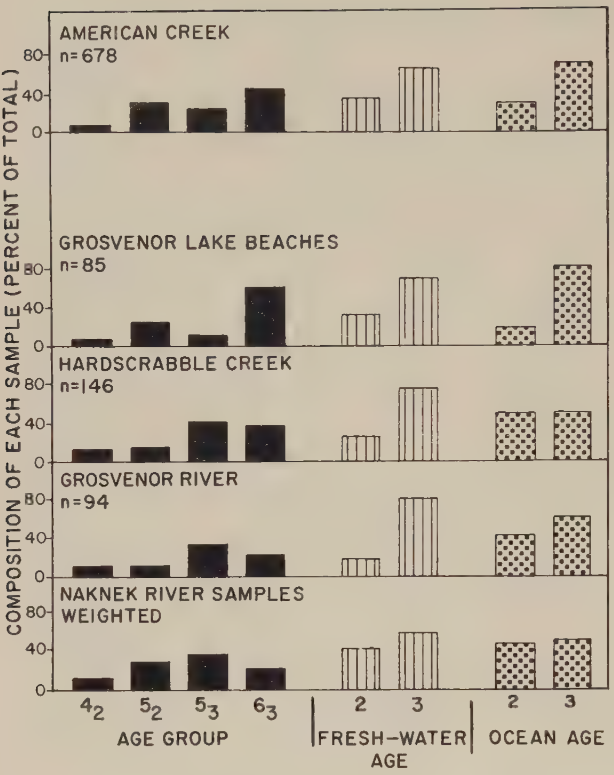

FIGURE 11.—Percent composition of sockeye salmon escapement for American Creek (Coville Lake) and three major spawning areas of Grosvenor Lake compared with overall Naknek system escapement, by age group and fresh-water and ocean age, 1962.

age on the major spawning grounds of the Naknek River system.

Most spawning ground samples contained a considerably higher proportion of the 5_3 age group and a lower proportion of the 5_2 group than did the trunk river samples. Only the Iliuk Arm, Grosvenor Lake beach, and American Creek samples contained a proportion of the 5_2 group approaching that of the river samples. It is notable that the samples from these three areas also contained almost twice the proportion of the 6_3 age group as did the river samples. Ocean-age samples from these three areas were characterized by predominantly 3-ocean fish in 1962. Practically all other spawning ground samples contained predominantly 2-ocean fish, many of them with twice the proportion that occurred in the river samples.

Fresh-water age samples from most areas contained a considerably smaller proportion of 2-fresh-water fish than did the Naknek Riv samples. Only the samples from stream N2 (9 fish) and the sample taken at the outlet Naknek Lake (80 fish) (table 7) had greater pr portions of 2-fresh-water fish. For the Nakn Lake spawning grounds as a whole there was lack of 2-fresh-water fish, primarily because the absence of the 5_2 age group.

TABLE 8.—*Numbers of fish in dominant age group sockeye salmon samples taken from the major spaw grounds of the Naknek River system, 1962*

Spawning area	Fish in age group—				T
	4_2	5_2	5_3	6_3	
Bay of Islands Creek	3	3	41	5	
Iliuk Arm beach	1	9	6	29	
Margot Creek	1	2	36	15	
Brooks River	3	1	30	5	
Naknek Lake outlet	54	5	20	0	
Grosvenor Lake beach	6	20	8	50	
Hardscrabble Creek	17	19	55	53	
Grosvenor River	8	8	30	45	
American Creek	35	193	149	295	
Total	128	260	375	497	1

Discussion

The absence of the 5_2 age group suggests i adequate sampling of the total Naknek escap ment on the spawning grounds. All know spawning grounds were surveyed and sampled i 1962, but only about half of the total escapemen counted on the Naknek River could be accounte for on the spawning grounds surveyed. It seem likely that some major spawning areas were no sampled and that these areas could have containe a high proportion of the 5_2 age group that was s prevalent in the river samples.

Until 1962 the Iliuk Arm beach area of Naknek Lake was not regarded as a probable spawnin ground. During the 1962 stream surveys in thi area, however, survey crews noted large number of fish jumping along a 1½- to 2-mile stretch o the southeast shoreline. These fish were presen after most of the tributary stream spawning had been completed, but because of the turbid water we could not definitely establish whether these fish actually spawned in this area nor could we estimate their number. Evidence suggests, however, that they spawned in the beach area Subsequent sampling of these fish showed that they were composed of a greater proportion of the 5_2 age group than most of the other spawning grounds sampled. It is likely that this population was sufficiently large to account for a substantial portion of the 5_2 age group represented in the Naknek River samples, but lacking in the samples from the other spawning grounds.

Other probable spawning areas in the Naknek system include the turbid Savonoski River (fig. 2) and most of its clear-water tributary streams and deepwater beach spawning areas as yet unknown. None of these were sampled in 1962.

Regardless of the spawning areas left unsampled, it seems clear from the evidence presented that there is segregation by age on the spawning grounds of the Naknek River system. This agrees with the conclusion reached by Koo and Smith (1960) for various spawning areas of the Kvichak River system in Bristol Bay.

Theoretically this segregation could be of great importance in managing individual spawning populations as they pass through the fishery. If certain spawning grounds are characterized by populations composed predominantly of fish of 2-ocean age and others of 3-ocean age, the effects of the gill net fishery, which is selective for large fish, would be unequal for each group. A knowledge of any consistencies in the age structure of individual spawning populations would, therefore, provide those charged with managing the Naknek sockeye salmon stocks with a means of gaging the possible effects of the fishery on these populations. Many years of data, however, will be required before consistencies in the age structure of individual spawning populations could show up.

The results presented above suggest two important lines of future investigation: (1) A complete survey of all beach and turbid water areas of the Naknek system for spawning areas that were previously undetected, and (2) continued study of segregation by age on the spawning grounds to uncover any consistencies in the age group structure of individual spawning populations.

SUMMARY

1. Tag and recovery techniques were used to determine the extent of segregation by time of occurrence for the individual spawning populations in the sockeye salmon run of Naknek River, Alaska. Salmon were tagged daily on the Naknek River at a site located about 24 miles above the mouth of the river. A different tag color combination was used to identify each day of tagging. Subsequent recovery or observations of tagged fish on the spawning grounds and the relative abundance of each color combination present provided the basis for determining the extent of segregation.

2. Results lead to the following conclusions: (*a*) Segregation of individual Naknek spawning populations by the time of occurrence in the trunk stream was minimal. As a consequence, most spawning grounds derived their fish from all parts of the run and, generally, in proportion to the size of the daily escapement. Exceptions were Brooks River, which received a disproportionate share of early-run spawners, and Grosvenor River, which seemed lacking in early-run fish. (*b*) The short duration of the Naknek run is probably the most reasonable explanation for the intermingling of most spawning groups. (*c*) Because of the lack of segregation in time, it is unlikely that spawning populations can be managed on an individual basis in the fishery. The Naknek sockeye salmon stocks will probably be most effectively managed, as a whole, by securing spawning escapement proportional to the daily abundance of fish in the fishery.

3. No seasonal trends in age composition could be described as characteristic of the Naknek run, probably because of intermingling of most of the spawning populations during the run.

4. Fish from all known spawning grounds of the Naknek system were sampled to determine the age composition of populations associated with the separate spawning areas. Spawning populations have age characteristics that differ significantly from one to another and, therefore, show segregation by age on the spawning grounds of the Naknek River system. Continued study of segregation by age on the spawning grounds is necessary for a number of years to determine if the age structure of specific spawning populations conforms to specific patterns. It is likely that major spawning population's as yet undetected and, therefore, not sampled in this experiment exist in the Naknek system. A thorough survey to locate and determine the magnitude and age characteristics of these populations, if any, is needed for a complete understanding of segregation and the productive importance of individual spawning areas within the Naknek system.

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SKIPJACK TUNA SPAWNING IN THE MARQUESAS ISLANDS AND TUAMOTU ARCHIPELAGO

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ABSTRACT

Spawning of skipjack tuna (*Katsuwonus pelamis*) in the Marquesas and Tuamotu areas was investigated by examining ova from 402 pairs of ovaries collected during exploratory fishing cruises, August 1956 to June 1958. Investigated were size at first spawning, spawning season, frequency of spawning, fecundity, use of the gonad index as a measure of maturity of skipjack, and the relation of stage of sexual development to schooling behavior.

The length at first spawning of skipjack in the two areas was found to be about 43 cm., although a few fish as large as 50.7 cm. apparently were not yet ready to spawn. Spawning activity reached a peak during November–April. The data indicate a possibility that individual skipjack may spawn more than once during a season. Number of ova extruded per spawning was estimated at 0.1 to 2 million. The gonad index could not be used as a measure of sexual development. Skipjack schools tended to have fish in a similar stage of sexual development.

From 1956 to 1959 the staff of the Bureau of Commercial Fisheries Biological Laboratory at Honolulu investigated the tuna resources of waters of French Oceania around the Marquesas Islands and the Tuamotu Archipelago. A study of the spawning of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), which appears to be the most abundant surface-schooling species of tuna in this area, was included in the investigations.

This study is based on the systematic microscopic examination and measurement of the ova in skipjack ovaries, generally following the method described by Clark (1934). Skipjack spawning studies, based generally on the examination of gonads or on the capture of larvae and juveniles, have been made in many different areas of the Pacific. On the basis of the examination of gonads, Matsui (1942) inferred that skipjack may spawn throughout the year in the vicinity of Palau; Marr (1948) concluded that spawning occurs in the northern Marshall Islands, and confirmed this by the capture of two juveniles; Yabe (1954) and Yao (1955) found evidence of spawning in the southern waters of Japan; Brock (1954) postulated that they spawn in Hawaii from late February, March, or April to the first part of September; Schaefer and Orange (1956) and Orange (1961) hypothesized that they spawn in the vicinity of the Revilla Gigedo Islands in the eastern Pacific; and Wade (1950a) found evidence of their spawning in Philippine waters.

By virtue of the capture of larvae and juveniles, Schaefer and Marr (1948) demonstrated the existence of a spawning ground off Central America; Wade (1950b and 1951) found further evidence that skipjack spawn in Philippine waters; Shimada (1951) deduced that spawning occurs around the Phoenix Islands; and Matsumoto (1958) showed that they spawn in a wide area in the central Pacific Ocean. The present study demonstrates the existence of yet another spawning locality in the Pacific.

NOTE.—Approved for publication Oct. 22, 1964.

MATERIALS AND METHOD

COLLECTION OF OVARIES

This study is based on 402 pairs of ovaries collected on seven exploratory fishing cruises from August 1956 through June 1958. The approximate locales of collection are shown in figure 1. Most of the ovaries were collected from fish caught at the surface by pole and line. This method of fishing, as used in the Hawaiian skipjack fishery, was described by June (1951).

Plans for all of the pole-and-line fishing cruises called for sampling 25 skipjack from each school fished in order to obtain an estimate of their size and sex composition. From the 25 fish thus selected, the first 5 females picked at random were cut open and their ovaries removed for examination. Skipjack were caught by pole and line from 92 schools during this study, and ovary samples were secured from fish from 81 of these schools. Longline fishing and incidental trolling provided the few remaining samples. A description of the longline fishing method was given Mann (1955).

The ovaries were preserved in about 10 perc formalin. At the time of collection a record made of the date, locality, method of fishing, the fork length of the fish.

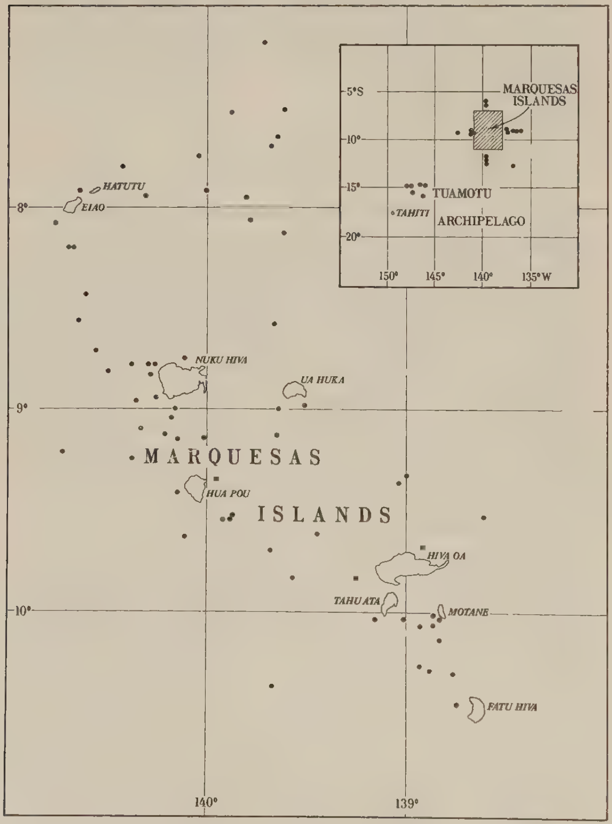

Figure 1.—Locations where skipjack ovaries used in this study were collected.

EXAMINATION OF OVARIES

Several investigators made detailed studies the distribution of mature ova within ovari June (1953) for yellowfin (*Thunnus albacare* Yuen (1955) for bigeye (*Thunnus obesus*); a Otsu and Uchida (1959) for albacore (*Thunn alalunga*). All showed that a representat sample of ova could be obtained anywhere alo the length of an ovary or from either member o pair.

Similarly, an analysis of variance of the me size of mature ova within a skipjack ovary in cated that they were homogeneously distribute Therefore, the following sampling method w adopted for this study. The formalin-preserv ovaries were weighed after excess moisture a tissue had been removed. A cross-section abo ⅛-inch thick was taken, usually from the midd of the right ovary, from which a wedge-shap (triangular) sample was cut. In many instanc it was not possible to distinguish the right ova from the left. In these instances the smaller the pair was selected for examination; it appeare that the right ovary was usually the smaller of t two. I assumed that the distribution of ov within the right and left ovaries is similar, as h been reported for the tuna cited above.

The ova from the triangular section were tease apart in a shallow dish and measured in a Sedg wick-Rafter counting chamber. Measurement were made with an ocular micrometer having magnification of 0.016 mm. per micrometer div sion. Since the ova were not perfectly spherica the diameter which was measured was the rando diameter that fell parallel to the lines in th counting chamber.

At the outset of the study, 300 randoml selected ova, 10 micrometer divisions (0.16 mm. or larger, were measured from each ovary in orde to characterize the size of ova at the differen developmental stages. Since this required a grea amount of time, and since the determinations o the stage of development of the ovaries wer based on the most developed ova, the sample siz was later reduced to a random sample of 25 of the most developed group. Following Snedecor (1946, p. 457), I analyzed the data on ova size distributions; my analysis showed that 25 was an adequate number to approximate the mean size.

DEVELOPMENTAL STAGES OF OVA

Four rather distinct developmental stages were recognized and designated as "early developing," "developing," "advanced," and "ripe". The early developing category includes ova which, at their most primitive, appear as simple transparent cells present in all ovaries. The larger ova in this stage contained a relatively large nucleus. The mean diameter of the early developng ova ranged from 0.16 to 0.33 mm. The ova assigned to the developing stage were completely opaque because of the deposition of yolk granules. Their mean diameter was 0.37 to 0.66 mm. The advanced stage comprised ova that were still relatively opaque in appearance and contained a cluster of small oil droplets to ova that were semitransparent and had a well-developed, bright yellow oil globule. The mean diameter of these ova was 0.49 to 0.74 mm. The collection had no ripe ovaries; however, a sample of ova from a running ripe skipjack caught on January 26, 957, was available for examination. This skipjack was caught by pole and line at 9°33′ S., 39°55′ W., about 10 miles southeast of the island f Hua Pou in the Marquesas. Its ova were used n an unsuccessful attempt at artificial fertilization nd were preserved and brought to the laboratory. They are almost perfectly spherical and transparent, with a distinct straw-colored oil globule. Fifty were measured. Their diameters were 0.85 to 1.12 mm., with a mean of 0.96 mm. The oil globule was about 0.14 mm. in diameter.

The sizes of these ripe ova are similar to those described by other investigators. Brock (1954) ound ripe ova from a skipjack in Hawaii to average 1.125 mm. in diameter. Yabe (1954) measured some ova from a ripe skipjack caught in the southern waters of Japan and found that they were 0.80 to 1.17 mm. in diameter, averaging .00 mm.

DEGREE OF MATURITY

Skipjack were classified according to the stage f development of the most developed group of va: the nomenclature used was the same as for the stages of ova development. Throughout this report, unless otherwise stated, the designations early developing, developing, advanced, and ripe will be used interchangeably to describe a skipjack, its ovaries, and the most developed ova contained therein.

The early developing category included ovaries as small as 2 g., from a sexually immature fish, and those (from adult fish) which were relatively large but which contained only early developing and a few residual ova. This category also included some ovaries containing ova that appeared to have attained the developing stage but had begun to degenerate. These ova were grayish, relatively soft, and easily broken.

TREATMENT OF DATA

Skipjack from the Marquesas and the Tuamotu areas were considered together in all aspects of this study, because I assumed that they belonged to the same population or at least were similar physiologically insofar as spawning was concerned. It would have been interesting to determine whether skipjack from the two areas did indeed have similar spawning habits; however, the samples from the Tuamotus were too few to treat that area separately. Of the 402 pairs of ovaries collected, 372 came from around the Marquesas and 30 from the Tuamotus.

SIZE AT FIRST SPAWNING

The approximate body length at first spawning was determined by arranging the lengths and the stage of development of all the skipjack used in this study into a frequency distribution (fig. 2). The smallest skipjack measured 39 cm. This fish had thin, ribbonlike ovaries which weighed 2 g. and contained only primitive ova. Presumably it had never spawned. The ovaries of a few fish, 43.7 to 50.7 cm. long, were classified as early developing and also showed no positive evidence of past spawning. A greater number in that size range, however, had either developing or advanced ovaries. The smallest fish that had advanced or developing ovaries was 43 cm. long. The few fish more than 55 cm. long that were classified as early developing either showed evidence of past spawning or at least of having attained a stage of development past early developing, for their ovaries contained residual or degenerating ova.

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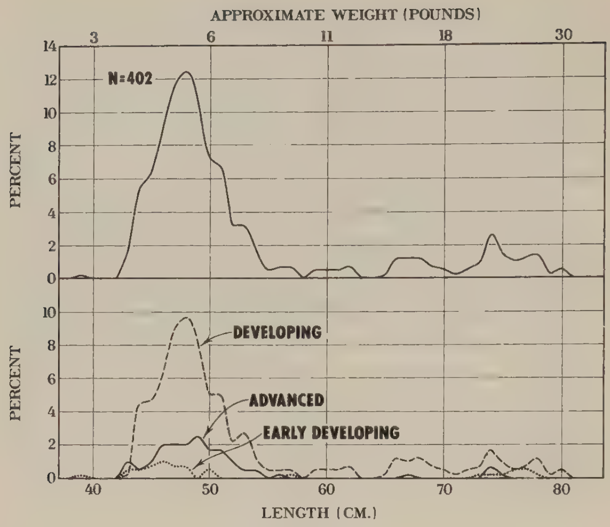

FIGURE 2.—Skipjack length-frequency distribution and stage of development.

It was noted earlier that one skipjack with running ripe ovaries had been caught. Unfortunately, the length of this specimen was not recorded. However, a sample from the school from which this fish was taken showed their size to range from 45.6 to 56.9 cm., and in all likelihood this specimen fell within this length range.

It seems from these observations that, although some skipjack as large as 50.7 cm. were apparently not ready to spawn, those in the Marquesas-Tuamotu areas are capable of first spawning when they are about 43 cm. long.

The size at first spawning has been determined for skipjack in other areas of the Pacific. Brock (1954, p. 102), discussing skipjack in Hawaii, states, "The smallest fish that possessed maturing ova during the spawning season were around 40 to 45 cm. long. Fish 35 to 40 cm. in length had ovaries that, with a few exceptions, seemed immature." In the southern waters of Japan, Yabe (1954) noted that no definite information was available because of the scarcity of data, but that the smallest skipjack in his samples with mature ova was 46.8 cm. long. In the eastern Pacific, Orange (1961) found the minimum size at first spawning for skipjack around the Revilla Gigedo Islands to be about 55 cm., and around the Cocos Island area about 40 cm.

From the above discussion it appears that the size at first spawning may vary with locality. Skipjack in the Marquesas and Tuamotus, in Hawaii, and in the southern waters of Japan seem to mature at about the same size, whil certain areas in the eastern Pacific they attai larger size before reaching maturity.

It is interesting that all samples from Marquesas and Tuamotus were composed marily of adult fish. The Hawaiian summer s jack fishery also exploits mostly adult fish (Br 1954, fig. 1). In the eastern Pacific, if the s frequency samples presented by Hennem (1957) are typical, the fishery depends on b juvenile and adult fish. The Japanese skipj fishery probably exploits adult as well as juve fish (Yabe, 1954; Yao, 1955).

SPAWNING SEASON

It would be relatively simple to determine spawning season of skipjack if all the ovar ripened at the same time and if ripe fish w readily taken. Small numbers then could examined to follow the development of ova to t time of spawning. My data show, however, t presence of a diversity of developmental stages any one period; therefore, another method had be employed to define the spawning season.

The temporal distribution of skipjack possessi ripe or advanced ovaries should give some in cation of the spawning season, the implicati being that these fish are actively spawning or ve close to spawning. The percentage distributi of skipjack by month of capture and stage development is presented in figure 3. Only tho larger than the size at first spawning, and ther fore, presumably only adult fish, were used in th analysis. All but one specimen in my collecti

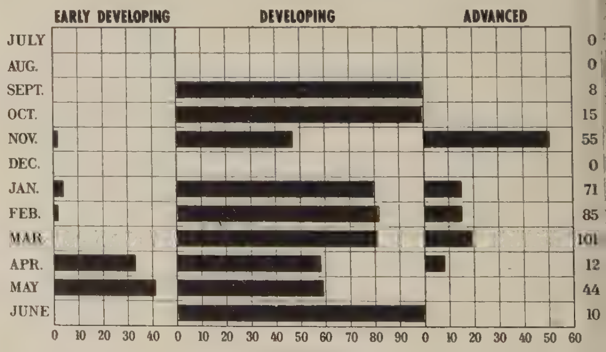

FIGURE 3.—Seasonal distribution of early developin developing, and advanced skipjack.

were included. As indicated earlier, aside from one running ripe fish, which was caught in January 1957, no ripe skipjack were available during the periods of sampling. Those in the advanced stage were found, however, in November, and January to April. This suggests that their major spawning season in this area is from about November through April.

The spawning season may be further defined by determining the temporal distribution of nonspawning; i.e., early developing skipjack. It was noted earlier that some classified as early developing possessed ovaries that either (1) contained only early developing ova, aside from a few residual ova from a previous spawning, or (2) contained ova that had reached the developing stage but were apparently degenerating. These observations suggest that during certain periods of the year the ovaries may revert to a dormant or early developing stage. A few skipjack classified as early developing were found in November, January, and February; however, the greatest numbers occurred in April and May, the months in which fish in the advanced stage were declining in number or were totally absent. I assumed that such a distribution of early developing and advanced skipjack indicated a decrease in spawning activity during these 2 months. However, the situation is probably more complex, since skipjack in all stages of development were found simultaneously, and fish with developing ovaries were found in all months sampled. In all probability, scattered spawning occurs throughout the year, but the peak activity is from November through April (or, roughly, the Southern Hemisphere summer). The results of a study of the distribution of skipjack larvae in this area, described by Nakamura and Matsumoto,[1] substantiate this conclusion. The larvae were caught in greater abundance contemporaneously with the greatest numbers of fish with advanced ovaries.

Skipjack spawning seasons in other areas, as in Hawaii, appear to be typically long. The season in Hawaii extends from late February, March, or April to the first part of September (Brock, 1954). Schaefer and Orange (1956) indicated that skipjack spawn in the vicinity of the Revilla Gigedo Islands from April to December, and that spawning is more intense in summer and fall. Concerning the fish in the Philippines, Wade (1951, p. 469) states, ". . . there are indications that the period from September to April, inclusive, may be the principal spawning period." The spawning season in the southern waters of Japan, however, is relatively short. Yao (1955) postulated that skipjack spawn during June–August in the waters south of Kyushu and the Ogasawara area.

FREQUENCY OF SPAWNING

The presence of two or more modes in ova-size frequency distributions and that of residual ova in ovaries containing mature ova have been used to hypothesize multiple spawning. Among investigators studying tuna, June (1953) concluded on the basis of such evidence that yellowfin in Hawaiian waters spawn more than once during a season. So did Brock (1954) for Hawaiian skipjack, Yuen (1955) for the bigeye in the Pacific, and Otsu and Uchida (1959) for the Pacific albacore.

The ova-diameter frequency distributions for skipjack in northeastern French Oceania were typically bimodal, or sometimes multimodal in the more advanced ovaries (fig. 4). Furthermore, residual ova were found in ovaries of 23 of the 72 skipjack that were judged to be in the advanced stage.

MacGregor (1957) discussed this problem of multiple spawning in some detail in an analysis of Pacific sardine fecundity. He disagreed with several criteria that have been used in the past to

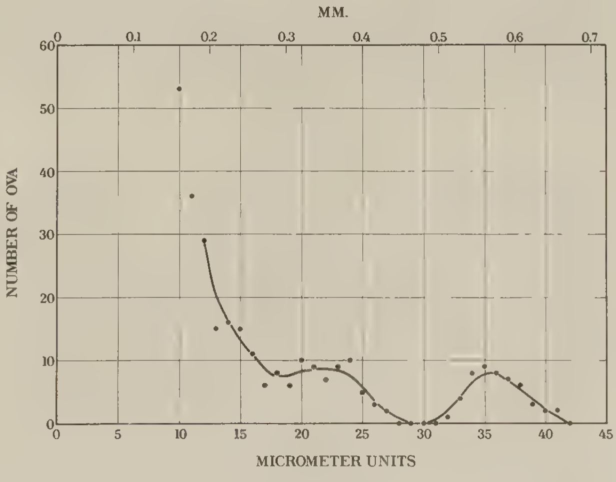

Figure 4.—Ova-diameter distribution for a developing skipjack ovary.

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[1] Nakamura, E. L. and W. M. Matsumoto. MS. Distribution of larval tuna in Marquesan waters. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. (Manuscript.)

hypothesize multiple spawning; he objected to the criterion of the presence of two or more modes in ova-size frequency distributions. He pointed out that the presence of two or more such modes in developing ovaries does not necessarily mean that all the groups mature and that multiple spawning will occur.

Support for MacGregor's contention may be found in Yabe's (1954) work on skipjack in Japanese waters. He noted that skipjack smaller than 47 cm. had relatively large ovaries from June to August, but that the relative size of the ovaries decreased after September. He suggested that the ovaries shrank without spawning having occurred.

As noted earlier, my data also show some ovaries that were classified as developing but contained what appeared to be degenerating ova; this finding, one may argue, is in agreement with MacGregor's thesis. It also may be argued, however, that these data merely indicate that there may be a cessation of spawning during part of the year and do not necessarily indicate that none of the intermediate-sized ova will be spawned. Furthermore, skipjack as small as 43 cm. possessed advanced ovaries which also had residual ova from a previous spawning. If their growth rate in this area is similar to that of the species in Hawaii (Brock, 1954), which is not entirely unreasonable since skipjack in both areas seem to reach adulthood at about the same length, then these small fish must have spawned no more than 3 or 4 months previously. Earlier than that they would not have been large enough to be sexually mature. These observations, although not conclusive, indicate the possibility of multiple spawning within a season for individual skipjack.

FECUNDITY

Four skipjack with fork lengths of 43 to 74 cm. and with advanced ovaries were selected for fecundity determinations. Small sections were obtained from each of the ovaries and weighed to the nearest thousandth of a gram. The number of ova in the most advanced group in the sample was determined and multiplied by the ratio of ovary weight to sample weight to get an estimate of the total number of mature ova in the ovary. The results are presented in table 1, which also includes results obtained by Yabe (1954) for skipjack in Japanese waters. Estimates of the number of ova extruded at one spawning ranged from
million to 2 million, with an indication that
number spawned is related to the size of the s
jack, the larger fish spawning more ova. Jos
(1963) made fecundity determinations for
skipjack taken from the eastern Pacific Oce
His estimates ranged from about 0.2 million
1.5 million ova per spawning for skipjack w
total lengths from 61.4 to 71.5 cm. Within
limits of his data, the size of the skipjack and
number of ova per spawning seemed to be relat
Among some of the other tuna, a relation betw
the number of ova spawned and size of fish w
found for the bigeye in the Pacific (Yuen, 19
and Hawaiian yellowfin (June, 1953).

TABLE 1.—*Results of skipjack fecundity determination*

Fish length	Ovary weight	Weight of sample	Advanced ova in sample	Estimat advance ova in ov (million
Centimeter	*Gram*	*Gram*	*Number*	*Numbe*
43.0	35	0.046	195	
46.8 [1]				
50.5	112	.089	330	
56.2 [1]				
67.9	202	.080	352	
75.0	303	.029	192	

[1] Data from Yabe (1954).

GONAD INDEX

Several investigators have discussed the poss
bility of using the relative ovary weight (ovar
weight×10^3/fish weight) as a measure of maturit
of tuna; e.g., June (1953), Yuen (1955), and Ots
and Uchida (1959). Schaefer and Orange (195
also used the relative ovary weight to measure th
maturity of skipjack, the only difference bein
that they used the cube of fish length instead
fish weight and a factor of 10^8 instead of 10
They called this relation the "gonad index,
which is defined as $G.I.=\frac{w}{L^3}\times 10^8$, where "G.I.
is the gonad index, "w" the weight of the ovarie
in grams, and "L" the fish length in millimeter
Schaefer and Orange plotted the gonad inde
against the 95th centile of the total ova-siz
frequency distribution and found a linear relation
the gonad index increasing with ova size, at leas
in their Area II of the eastern Pacific.

I calculated the gonad index for all the skipjac
in my collection. Because only a sample of th
most developed group of ova was measured, thei

mean sizes were plotted against the gonad index in lieu of the 95th centile of the total ova-size frequency distribution. This difference should not affect greatly the comparison of my results with those of Schaefer and Orange.

Figure 5 is a scatter diagram showing my results, with the regression line obtained by Schaefer and Orange for their Area II data superimposed. Schaefer and Orange concluded that the gonad index was a reasonably reliable measurement of the degree of ova development; however, the largest gonad index they found was about 36, as compared to my 96. My data fit Schaefer and Orange's regression line fairly well up to a gonad index of 36. Above this value the relation seems to break down. There is a big overlap in gonad index between developing and advanced ovaries; therefore, it was not possible to make any inferences about the stages of development of skipjack in this area from the gonad index.

STAGE OF SEXUAL DEVELOPMENT AND SCHOOLING BEHAVIOR

As mentioned earlier, the sampling of skipjack by pole-and-line fishing was such that each sample represented fish captured from a single school. This circumstance made it possible to examine the within-school distribution of developmental stages.

A gross examination of the data (table 2) indicates that skipjack in the different stages of development were not distributed randomly within schools. Although fish in all stages of sexual development were found simultaneously in certain months, there was no instance in which all three stages of development were found within a school. Most of the schools were represented by skipjack in a single stage of development. A contingency test of homogeneity (Hoel, 1954, pp. 172–175) was applied to the data, testing the hypothesis that, with respect to stage of sexual development, skipjack are distributed randomly within schools. The probability ($X^2=510$, df=144) of obtaining the observed distributions by chance alone was less than 1 in 100. I conclude that there was indeed a relation between schools and stage of sexual development. The fact that fish of similar stages of sexual development tended to occur together, as well as the fact that those in several stages of development were found in a number of months, should be considered in the design of any study of spawning. Obviously, examination of a large number from only a few schools could lead to erroneous conclusions.

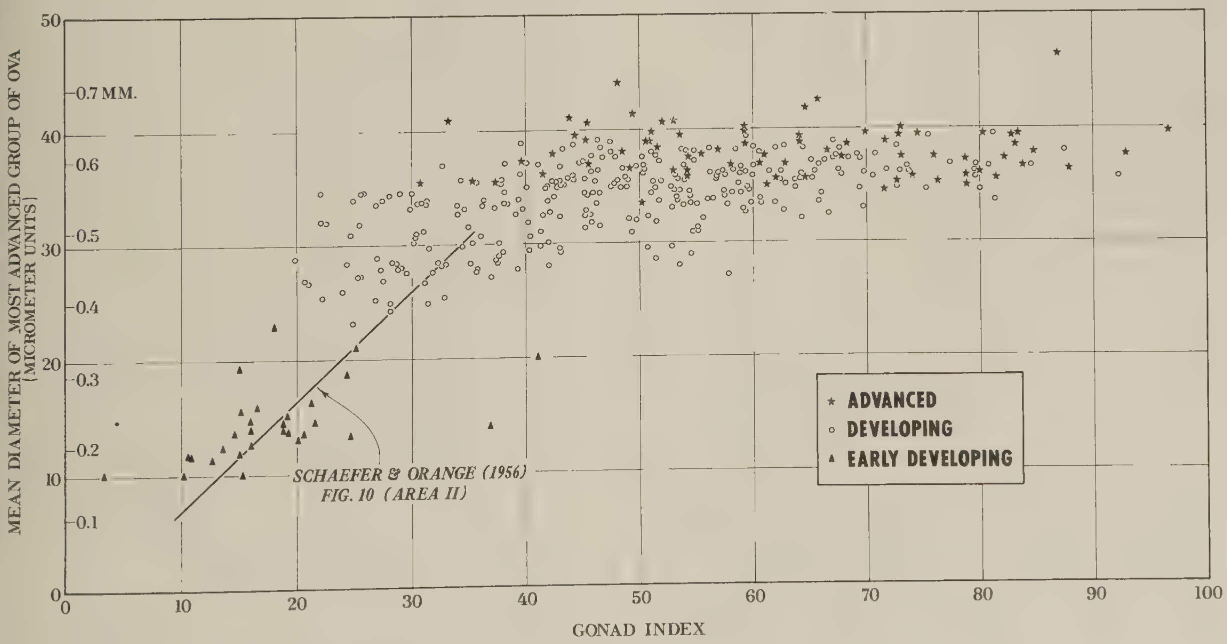

FIGURE 5.—Gonad index and mean diameter of largest group of ova.

TABLE 2.—*Numbers of skipjack in each stage of development in samples from single schools*

School	Stage of sexual development			Total
	Early developing	Developing	Advanced	
1	0	5	0	5
2	0	5	0	5
3	0	5	0	5
4	0	4	1	5
5	0	5	0	5
6	0	5	0	5
7	0	5	0	5
8	0	5	0	5
9	0	5	0	5
10	1	4	0	5
11	0	5	0	5
12	0	4	1	5
13	0	0	5	5
14	0	5	0	5
15	0	3	2	5
16	0	5	0	5
17	0	5	0	5
18	0	5	0	5
19	0	5	0	5
20	0	2	3	5
21	0	2	3	5
22	0	2	3	5
23	0	1	4	5
24	0	2	3	5
25	0	5	0	5
26	0	5	0	5
27	0	5	0	5
28	1	4	0	5
29	0	0	5	5
30	0	4	1	5
31	0	3	2	5
32	0	5	0	5
33	0	0	5	5
34	0	0	5	5
35	0	0	5	5
36	0	2	3	5
37	0	3	2	5
38	0	5	0	5
39	3	2	0	5
40	0	5	0	5
41	0	5	0	5
42	0	0	5	5
43	0	5	0	5
44	0	2	3	5
45	0	5	0	5
46	0	5	0	5
47	1	4	0	5
48	0	4	1	5
49	0	5	0	5
50	0	5	0	5
51	0	4	1	5
52	0	5	0	5
53	0	5	0	5
54	0	5	0	5
55	0	5	0	5
56	0	5	0	5
57	0	5	0	5
58	0	5	0	5
59	0	4	1	5
60	0	5	0	5
61	0	4	1	5
62	4	1	0	5
63	1	4	0	5
64	5	0	0	5
65	0	5	0	5
66	0	5	0	5
67	0	5	0	5
68	1	4	0	5
69	5	0	0	5
70	2	3	0	5
71	5	0	0	5
72	0	5	0	5
73	0	5	0	5
Total	29	271	65	365

As far as could be determined, there is very little in the literature regarding skipjack sexual development and schooling behavior. What are the causes of their apparent segregation by stage of sexual development? One possibility may be that skipjack about to spawn seek one another out, resulting in schools of similarly developed i viduals. This explanation appears reasonable, such a situation is probably more efficient spawning purposes than a random distributio spawning and nonspawning fish. Another ex nation is that skipjack schools are relatively st aggregations, with individuals in the gr responding similarly to the environment a therefore, developing similarly. However, on basis of his size analysis of skipjack schools Hawaii, Brock (1954) concluded that their co position is not stable. The pattern of tagged returns in Hawaiian waters seems to substanti Brock's conclusion (Yamashita[2]). There proba is no simple explanation for this phenomen Undoubtedly there are many factors that influe the schooling behavior of skipjack, and the served similarity of sexual development of the f in the schools is probably a manifestation of complex of factors.

SUMMARY

1. This study is based on the microscopic exa ination of ova from 402 pairs of ovaries collect from skipjack caught on exploratory fishing cruis from August 1956 through June 1958 around t Marquesas Islands and Tuamotu Archipelago.

2. The ova, ovaries, and skipjack were class fied as being in the "early developing," "develo ing," "advanced," and "ripe" stages of develo ment according to the physical characteristics the most developed group of ova. Early develo ing ova ranged in appearance from simple tran parent cells to cells with a well-developed nucleu developing ova were opaque because of the de osition of yolk; advanced ova were opaque semiopaque and contained a cluster of oil droplet or a single well-developed oil globule; ripe ova wer almost perfectly spherical and transparent an contained a distinct straw-colored oil globule.

3. Skipjack in the Marquesas and Tuamot areas are capable of first spawning when they ar about 43 cm. long.

4. Scattered spawning may occur throughou the year, judging from the occurrence of develop ing skipjack in all months of sampling. Th major spawning season, however, appears to b from November through April.

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[2] Yamashita, Daniel T. Ms. Results of Hawaiian skipjack tagging. I files of the Bureau of Commercial Fisheries Biological Laboratory, Honolul (Manuscript.)

5. Although no conclusive statements can be made about the frequency of spawning of individual skipjack, the data indicate a possibility of more than one spawning per season.

6. Estimates of fecundity of skipjack ranged from 0.1 to 2 million ova per spawning.

7. It was not possible to make any inferences about the stage of development from the gonad index of skipjack.

8. A contingency test of homogeneity showed that there was a relation between skipjack schools and stage of sexual development; i.e., there was a tendency for skipjack in similar stages of sexual development to be found together in schools.

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FOOD OF YOUNG-OF-THE-YEAR WALLEYES IN LAKE ERIE

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ABSTRACT

Stomach contents were examined for 794 young-of-the-year (O-group) walleyes (*Stizostedion vitreum vitreum*) captured by trawls at 17 locations in western Lake Erie in June-November 1962. Food organisms were found in 92.5 percent of the stomachs. Food varied with geographic location and season of capture, but within areas and seasons, selection for certain species and sizes of prey was strong. Walleyes from the extreme western end of Lake Erie fed primarily on gizzard shad and alewives during the summer and shifted to emerald shiners during the fall. The stomach contents of walleyes from the Island region changed from mainly yellow perch during the summer to emerald shiners by the end of the year. Walleyes collected east of the Islands had consumed only smelt and yellow perch. The numbers of forage species caught with walleyes in trawls showed little correlation with the representation of these species in walleye stomachs. Walleyes fed on the smallest individuals of each species regardless of species preferences.

Among the fishes of primary economic importance in Lake Erie, the cisco or lake herring (*Coregonus artedi*), the whitefish (*C. clupeaformis*), the sauger (*Stizostedion canadense*), and the blue pike (*S. vitreum glaucum*) have become commercially unimportant, mostly in recent years. The last remaining "high-priced" fish left to the industry—the walleye (*S. vitreum vitreum*)—has also declined to a remnant population which fluctuates widely in abundance. The commercial catch (United States and Canadian) of walleyes has declined from a peak of 15,405,000 pounds in 1956 to a low of 717,000 pounds in 1962. The decline has been accompanied by demands for management of the fishery to restore and maintain abundance. Recent studies of the life history of the walleye were begun in 1957 to provide information essential to management. This report on feeding of young-of-the-year (O-group) walleyes at various seasons of the year and at different locations in western Lake Erie is a contribution to these studies.

MATERIALS AND METHODS

The contents were examined of 794 stomachs from O-group walleyes of the 1962 year class collected in western Lake Erie at 17 locations in June–November 1962 (fig. 1). All collections were from U.S. waters and were made during routine trawling to ascertain the relative success of the hatching and survival of commercial and other species. The fish were caught in semiballoon bottom trawls by Bureau of Commercial Fisheries vessels, *Musky II* (523 fish), *Kaho* (35), and an outboard-motor boat (233), and the Ohio Division of Wildlife vessel *Explorer* (3). The walleyes were preserved whole in 20 percent formalin after their abdomens had been slit; examinations and measurements were made in the laboratory. Food organisms were identified to the lowest taxonomic level possible. Stomach contents

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Note.—Approved for publication Oct. 14, 1964.
This research was completed at the Biological Field Station, Sandusky, Ohio.

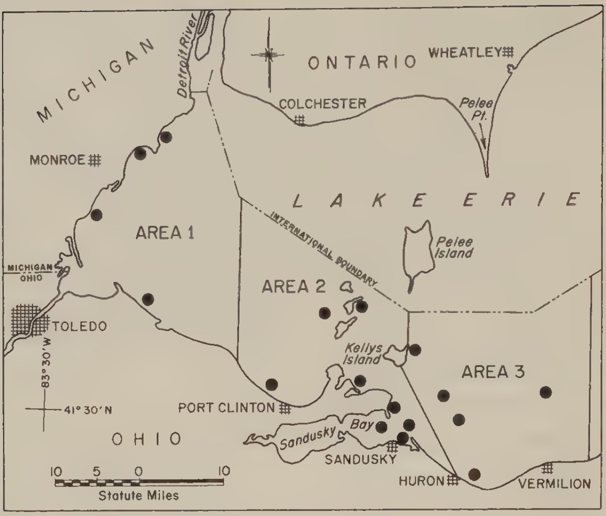

Figure 1.—Map of western Lake Erie showing locations where young-of-the-year walleyes were collected and areas by which data were analyzed. Dots represent collection locations.

were measured volumetrically by water displacement in a cylinder graduated to 0.1 ml. Items with a volume less than 0.1 ml. were listed as "trace". The entire stomach contents of 176 walleyes (41–74 mm. long) caught in June were examined with a dissecting microscope. No volumetric measurements were made of the food of these fish.

Counts were made of the O-group fish of the following species that were caught in the trawl hauls with the walleyes: Gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudohareng* American smelt (*Osmerus mordax*), emerald sh (*Notropis atherinoides*), spottail shiner (*N. h sonius*), trout-perch (*Percopsis omiscomayc* white bass (*Roccus chrysops*), yellow perch (*Pe flavescens*), and sheepshead or freshwater dr (*Aplodinotus grunniens*).

Data on food are presented separately for e of three areas in which walleyes were collec (fig. 1). Although the boundaries are somew arbitrary, each area differs ecologically from others and each has its own characteristic f fauna.

FOOD OF YOUNG WALLEYES IN DI FERENT AREAS

The food of young-of-the-year walleyes in La Erie varied with geographic location and seas of capture, but, within an area and season, sele tion for certain species and sizes of prey was stron In general, little correlation existed between t numbers of various forage species present in t same catches with walleyes and the representati of these species in walleye stomachs.

Extreme Western Lake Erie (Area 1)

Food organisms were found in 94.7 percent of t 189 walleye stomachs (table 1). Gizzard sha and alewives were the principal food in July Together they made up 72.7 percent of the tot volume; gizzard shad occurred in 30.6 percent an alewives in 20.7 percent of the stomachs contain ing food. These species represented only 4.1 per

Table 1.—*Food of young-of-the-year walleyes in extreme western Lake Erie in July, August, and October, 1962*

[Expressed in percentage of total volume (PV) and percentage frequency of occurrence (PO). Percentage frequencies based on numbers of stomachs containin food]

Food item	Dates of capture					
	July 17–24		August 14–16		October 15–18	
	PV	PO	PV	PO	PV	PO
Insects:						
Tendipes pupae	<0.1	0.1	<0.1	13.9		
Tendipes larvae			<.1	2.8		
Fish:						
Alewife	32.7	20.7	16.7	8.3		
Emerald shiner			47.0	47.2	99.7	100.
Gizzard shad	40.0	30.6	23.7	13.9		
Smelt	1.6	.9				
Spottail shiner	.3	.9				
Yellow perch	10.0	9.0	6.7	5.2		
Unidentifiable remains	15.4	53.2	5.9	33.3	.3	7.
Number of stomachs	120		37		32	
Number of stomachs empty	9		1		4	
Average total length (mm.)	108		157		226	

TABLE 2.—*Young-of-the-year fishes taken in the same trawl hauls as walleyes (1962)*

[Expressed as percentage of total trawl catches in each indicated period [1]; no data for Area 3 because walleyes east of the Islands were taken in large-mesh trawls]

Dates of capture	Yellow perch	Emerald shiner	Gizzard shad	Alewife	Spottail shiner	White bass	Sheeps-head	Trout-perch	Smelt
	Extreme western Lake Erie (Area 1)								
ly 17–24	39.2	----------	1.2	2.9	13.0	43.4	0.1	----------	0.2
ug. 14–16	16.9	0.4	5.4	5.5	9.3	58.5	3.6	0.3	.1
ct. 15–18	66.3	12.4	<.1	4.2	14.7	.9	.2	.6	.7
	Island region (Area 2)								
une 25–27	97.1	----------	----------	----------	----------	2.5	----------	0.2	0.2
ly 2–18	99.0	----------	0.7	<0.1	0.1	.2	----------	----------	----------
ly 25–Aug. 1	38.8	----------	11.9	.8	30.8	16.6	1.1	----------	<.1
ug. 20–30	79.6	----------	1.2	.8	12.7	4.1	<.1	.4	1.2
ept. 18–19	17.9	4.1	7.4	1.4	47.2	13.6	5.9	1.0	1.5
ct. 29–Nov. 1	73.0	2.2	.1	.6	19.3	.4	1.9	1.9	.6

[1] Numbers of young-of-the-year walleyes caught are given in table 1 and table 4.

ent of the total number of fish taken in the trawl
able 2). In contrast, white bass made up 43.4
ercent of the total number of O-group fish in the
awl catches from which the walleyes were ob-
ained but none were found in walleye stomachs.
ellow perch composed 39.2 percent of the trawl
atches but were in only 9.0 percent of the stom-
hs. The consumption of smelt and spottail
iners was negligible. No emerald shiners had
een eaten.

Gizzard shad and alewives were being sup-
lanted by other prey in stomachs of walleyes cap-
ured August 14–16. The volume of the two
ecies in stomachs had dropped to 40.4 percent
nd the frequency of occurrence was only 13.9
ercent for the gizzard shad and 8.3 percent for the
ewife. Emerald shiners had entered strongly
to the diet; they made up 47.0 percent of the
olume and occurred in 47.2 percent of the stom-
hs. Emerald shiners were scarce, nevertheless,
trawl catches (0.4 percent of the total catches).
he number of gizzard shad and alewives com-
ined had increased to 10.9 percent of all fish
ught, even though they had decreased in im-
ortance as food for walleyes. White bass, still
e most abundant forage species available, had
ot been eaten.

The shift in food from gizzard shad and alewives
emerald shiners was complete in October when
e identifiable stomach contents of 32 walleyes
ontained only emerald shiners. Emerald shiners
ad increased to 12.4 percent of the total catch
trawls in mid-October. Young-of-the-year
ellow perch, although now the most available
rage fish (66.3 percent of the total trawl catches), had not been eaten. Walleyes apparently sought more emerald shiners as the gizzard shad and alewives grew to a size that made them unsuitable prey (table 3).

Insects were eaten most commonly in August when the percentage frequencies of occurrence of pupae and larvae of the midge *Tendipes* were 13.9 and 2.8 percent, respectively. *Tendipes*, however, constituted a negligible amount of the total volume

TABLE 3.—*Comparison of total lengths (mm.) of young-of-the-year fish caught in trawls in extreme western Lake Erie and those taken from walleye stomachs (1962)*

Species and item	July 17–24		Aug. 14–16		Oct. 15–18	
	Trawls	Stom-achs	Trawls	Stom-achs	Trawls	Stom-achs
Alewife:						
Average length	48	42	89	56	117	--------
Range of length	33–69	36–47	64–102	52–60	76–147	--------
Number	256	8	91	3	141	0
Emerald shiner:						
Average length	--------	--------	51	49	69	55
Range of length	--------	--------	38–61	45–54	51–86	48–65
Number	0	0	100	4	339	42
Gizzard shad:						
Average length	56	46	102	55	157	--------
Range of length	48–76	35–50	79–130	49–64	135–193	--------
Number	13	5	40	4	141	0
Sheepshead:						
Average length	--------	--------	64	--------	109	--------
Range of length	--------	--------	33–89	--------	61–142	--------
Number	0	0	98	0	49	0
Smelt:						
Average length	45	--------	53	--------	69	------
Range of length	43–46	--------	51–58	--------	53–94	--------
Number	2	0	6	0	41	0
Spottail shiner:						
Average length	43	--------	51	--------	74	--------
Range of length	20–69	--------	38–64	--------	58–91	--------
Number	311	0	130	0	166	0
White bass:						
Average length	36	--------	69	--------	104	--------
Range of length	20–84	--------	43–86	--------	69–157	--------
Number	308	0	97	0	44	0
Yellow perch:						
Average length	53	36	66	53	81	--------
Range of length	41–74	33–42	58–76	53	66–97	--------
Number	482	6	142	1	219	0

of food. No other insects were present in the stomachs of walleyes from this area.

Island Region (Area 2)

Of the 562 walleyes collected from Area 2 (table 4) the late June sample of 176 individuals (mean length 55 mm.) required special treatment. All stomach contents of these small fish were examined with a dissecting microscope. The major food at this time was unidentifiable fish fry (frequency of occurrence—65.5 percent). Many of the fry probaby were yellow perch but positive identification was impossible, because of their small size. *Leptodora kindtii* appeared in 16.5 percent of the stomachs. Consumption of *Diaptomus*, *Cyclops*, and *Daphnia* was limited as was also that of unidentifible midge larvae and pupae. Ewers (1933) found *Leptodora* the most common of the Entomostraca in the diet of young walleyes and blue pike in western Lake Erie. The stomachs of 23 walleyes caught in the latter part of July 1929, and examined by Boesel[1] contained 82.9 percent Entomostraca and 17.1 percent fish by volume.

The 61 walleyes captured July 2–18 had been feeding entirely on fish fry. Yellow perch comprised 92.3 percent of the total volume. Seemingly little other food was available to small walleyes in this area at this season. Trawl catches in which the walleyes were taken consisted of 99.0 percent O-group yellow perch.

Young-of-the-year walleyes in other lakes of the Midwest consume large quantities of yellow perch. Eschmeyer (1950) found yellow perch in 42.1 percent of the stomachs of O-group walleyes of Gogebic Lake, Mich., during June 24 to July 10, 1941. Yellow perch also made up 68 percent of the total volume of food. Yellow perch constituted 77 percent by volume of the stomach contents of O-group walleyes in Mille Lacs Lake, Minn., in June–September (Maloney and Johnson, 1957).

The 219 walleyes taken July 25 to August 7 had eaten a diversity of organisms. Yellow perch continued to be the major food (total volume—64.3 percent; frequency of occurrence—72.3 percent). They were also the most available prey

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[1] Boesel, M. W. 1929. A preliminary report on the food of certain insect feeding fishes of Lake Erie. MS., Department of Zoology, Ohio State University, 30 pp.

TABLE 4.—*Food of young-of-the-year walleyes in the Island region in June–November 1962*

[Expressed in percentage of total volume (PV) and percentage frequency of occurrence (PO). Percentage frequencies based on numbers of stomachs containing food]

Food item	Dates of capture											
	June 25–27 PO[1]	July 2–18		July 25–Aug. 7		Aug. 20–30		Sept. 18–19		Oct. 29–Nov. 1	
		PV	PO	PV	PO	PV	PO	PV	PO	PV	PO
Algae	0.5										
Copepods:											
Diaptomus oregonensis	.5										
Diaptomus spp	.5										
Cyclops vernalis	1.9										
Cyclops spp	2.9										
Cladocerans:											
Daphnia retrocurva	1.9										
Daphnia galeata	.5										
Daphnia spp	1.5										
Leptodora kindtii	16.5										
Unidentifiable remains	.5										
Insects:											
Tendipes pupae				<0.1	7.0	<0.1	1.8				
Tendipes larvae				<.1	.5						
Unidentified midge pupae	2.4										
Unidentified midge larvae	3.4										
Ichneumonidae				<.1	.5						
Fish:											
Alewife				12.1	6.1						
Emerald shiner				4.5	3.3	3.0	3.5	9.3	22.9	93.0	88.8
Gizzard shad				12.1	4.2	.8	1.8	28.0	17.1		
Percina spp				.1	.5						
Smelt				.6	.9			1.5	8.6		
Spottail shiner				1.5	1.4						
Yellow perch	1.5	92.3	58.6	64.3	72.3	91.5	84.2	60.4	65.7	7.0	11.1
Unidentifiable fry	65.6	7.7	55.2								
Unidentifiable remains				4.8	31.0	4.7	19.3	.8	8.6	<.1	11.1
Number of stomachs	176	61		219		60		36		10	
Number of stomachs empty	27	3		6		3		1		1	
Average total length (mm.)	55	79		132		183		214		239	

[1] Volumes not measured in this collection.

(38.8 percent of all fish taken by trawl). Although gizzard shad and alewives made up 24.2 percent of the total volume of food, they were present in relatively few stomachs. Similarly, few spottail shiners had been eaten (frequency of occurrence—1.4 percent) even though they were readily available (30.8 percent of the trawl catches). Emerald shiners were not taken by the trawl but were in 3.3 percent of the stomachs. *Tendipes* pupae were more prominent at this time than in any other period (frequency of occurrence—7.1 percent). Maloney and Johnson (1957) reported that dipterous larvae occurred in the stomachs of walleyes taken in August in Lake Winnibigoshish, Minn.

Yellow perch made up the bulk of the food of the walleyes captured in the Island area, August 20–30 (total volume—91.5 percent; frequency of occurrence—84.2 percent). Gizzard shad had almost disappeared from the stomachs (total volume—0.8 percent). Again, emerald shiners had been eaten but were not in the trawl catches. Walleyes may have been seeking out this minnow. On the other hand, trawl catches may not provide an exact index of relative abundance of emerald shiners because this fish occasionally frequents the surface waters and hence becomes unavailable to bottom trawls.

The importance of yellow perch had begun to decline by September 18–19 (total volume—60.4 percent; frequency of occurrence—65.7 percent); perch were being supplanted by emerald shiners (total volume—9.3 percent; frequency of occurrence—22.9 percent). Trawl catches indicated that the availability of yellow perch had decreased while that of the emerald shiners had increased (table 2).

The few walleyes caught between October 29 and November 1 showed a further shift from yellow perch (total volume—7.0 percent; frequency of occurrence—11.1 percent) to emerald shiners (total volume—93.0 percent; frequency of occurrence—88.8 percent). Doan (1941) stated that emerald shiners constituted 82 percent of the volume of food eaten by 62 walleyes, 10–17 inches long, caught at Put-In-Bay, Ohio, in November and December 1940.

Evidence from extreme western Lake Erie (Area 1) suggests that the walleye prefers gizzard shad or alewives during its early months of life, even though ample numbers of young yellow perch (and other species) of suitable size are available. It is apparent from the fish taken in the Islands region (Area 2), however, that where yellow perch almost completely dominate the food supply, the walleye can and does feed heavily upon them. The shift to emerald shiners that occurred in the late summer and autumn in both Areas 1 and 2 may be traceable to different causes. In Area 1, the emerald shiners became prominent in the food of walleyes when the gizzard shad and alewives became too large to eat. In Area 2, the change probably reflects species rather than size preference since both the emerald shiners and the yellow perch captured in October were about the same size (table 5).

East of the Island Region (Area 3)

Forty-three O-group walleyes were collected off Huron and Vermilion, Ohio, and east of Kelleys Island in July, August, September, and October. The 38 fish that had food in their stomachs had eaten almost exclusively smelt and yellow perch (table 6). Yellow perch were the only food of walleyes in the small July collection. Some smelt were eaten in August, and by September this species had become the only food in almost all stomachs. No suitable records are available of the relative numbers of O-group fish living with the walleyes because most were taken in trawls with large-mesh cod ends that permitted the escape of most small fish. A cursory examination of the catches did reveal, however, that the bulk of forage available to the walleyes east of the Islands consisted of smelt and yellow perch in all seasons.

ACKNOWLEDGMENTS

The Bureau of Commercial Fisheries vessel *Kaho* and the Ohio Division of Wildlife vessel *Explorer* collected walleyes for stomach analysis. Jarl Hiltunen assisted in the identification of the immature midges, and LaRue Wells helped identify crustaceans. Vernon C. Applegate advised in the preparation of the manuscript.

TABLE 5.—*Comparison of total lengths (mm.) of young-of-the-year fish caught in trawls in the Island region and those taken from walleye stomachs (1962)*

Species and item	July 2–18		July 25–August 7		August 20–30		September 18–19		Oct. 29–Nov. 1	
	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs
Alewife:										
Average length	51		79	50			97			
Range of length	28–61		64–89	46–59			61–117			
Number	111	0	54	8	0	0	15	0	0	0
Emerald shiner:										
Average length				42		44		49	66	62
Range of length				37–45		44		43–55	56–76	55–65
Number	0	0	0	3	0	1	0	8	100	9
Gizzard shad:										
Average length			84	54			102	65		
Range of length			58-117	44–64			61–147	57–75		
Number	0	0	174	6	0	0	253	6	0	0
Sheepshead:										
Average length			69							
Range of length			30–99							
Number	0	0	193	0	0	0	0	0	0	0
Smelt:										
Average length				35	53			48		
Range of length				30–40	46–58			45–53		
Number	0	0	0	2	4	0	0	3	0	0
Spottail shiner:										
Average length	38		43	35	53		58		76	
Range of length	25–56		28–58	27–40	38–74		51–71		51–91	
Number	87	0	209	4	158	0	104	0	86	0
White bass:										
Average length	38		56		53		109		84	
Range of length	25–56		28–81		41–79		51–147		53-124	
Number	126	0	298	0	152	0	209	0	78	0
Yellow perch:										
Average length	41	25	48	37	58	49	71	51	71	50
Range of length	30–51	23–28	30–76	26–46	48–76	42–61	56–91	43–64	53–94	50
Number	121	6	573	79	171	48	75	45	186	1

TABLE 6.—*Food of young-of-the-year walleyes captured in Area 3 in July, August, September, and October, 1962*

[Expressed in percentage of total volume (PV) and percentage frequency of occurrence (PO). Percentage frequencies based on numbers of stomachs containing food]

Food item	Dates of capture							
	July 19		Aug. 23-30		Sept. 6–26		Oct. 10	
	PV	PO	PV	PO	PV	PO	PV	PO
Smelt			16. 1	50. 0	93. 3	63. 6	95. 7	90. 9
Yellow perch	100. 0	100. 0	83. 9	100. 0			4. 3	4. 5
Unidentifiable fish remains					. 7	36. 4	<. 1	4. 5
Number of stomachs	4		2		15		22	
Number of stomachs empty	1		0		4		0	
Average total length (mm.)	82		174		218		236	

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EFFECT OF THE SPAWNING BED ENVIRONMENT ON REPRODUCTION OF PINK AND CHUM SALMON[1]

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ABSTRACT

Mortality of 5 brood years of pink salmon, *Oncorhynhus gorbuscha,* and chum salmon, *O. keta,* in spawning beds of three Southeastern Alaska streams was studied. Eggs and larvae were sampled periodically, and mortality was associated with certain environmental factors: The supply of dissolved oxygen, the stability of spawning beds, and freezing.

Total mortality between spawning and fry emergence typically varied between 75 and 99 percent in the study areas. High mortality occurred during low and high stream discharge and freezing air temperatures. Mortalities ranging from 60 to 90 percent of deposited eggs occurred in association with low dissolved oxygen levels during and after the spawning period. Movement of gravel in certain instances was associated with the removal of 50 to 90 percent of eggs and larvae present in spawning beds. Freezing caused up to 65 percent mortality of eggs and larvae in one stream.

Low dissolved oxygen levels occurred once in 5 years. This occurrence was associated with unusually low water during spawning in late summer. Mortality during periods of heavy precipitation was highly variable. In one instance, a 90-percent mortality occurred where wood debris was deposited within the high water channel. Wood debris floating over spawning beds was not damaging to eggs and larvae. There were several instances where mortality estimated at almost 50 percent occurred with no evidence that deposited wood debris shifted position. High mortality from freezing occurred only in the stream having the lowest minimum discharge.

Pink salmon, *Oncorhynchus gorbuscha*, and chum almon, *O. keta*, are the only species of Pacific almon in North American streams using fresh water[2] solely for spawning. The young of these species, with minor exceptions, migrate to sea soon after emerging from spawning beds, while the young of chinook salmon, *O. tshawytscha;* sockeye, O. *nerka;* and coho, *O. kisutch*, may remain in fresh water for many months.

Adult pink and chum salmon commonly migrate into coastal streams to spawn in summer and early autumn. They excavate pockets in riffle areas and deposit and bury their eggs in the bottom. Surviving embryonic and larval salmon remain in the spawning bed for periods up to 8 months, and fry usually emerge and migrate seaward the spring after spawning.

The spawning bed protects eggs and larvae against predators, light, displacement, and mechanical injury. Despite this protection, mortality from time of egg deposition to fry emergence commonly exceeds 75 percent.

Estimates of total fresh-water mortality of pink and chum salmon have been published for McClinton, Morrison, Nile, and Hook Nose Creeks, British Columbia (Pritchard, 1948; Neave, 1953;

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[2] Includes intertidal areas periodically inundated by salt water or brackish ater.

Hunter, 1959); and Sashin Creek, Southeastern Alaska (Merrell, 1962). For the brood years studied, total mortality in these streams ranged from 76 to 99.9 percent. Although these estimates fail to differentiate among mortalities occurring during (1) adult migration, (2) egg and larval development, and (3) fry migration, other evidence indicates that the largest portion of total fresh-water mortality occurs between the time eggs are deposited and fry emerge.

Typical results are seen in mortality studies at Hook Nose Creek (Hunter, 1959). Although Hunter found that total deaths varied considerably from year to year, losses before spawning appeared to be consistently small. The number of fry consumed by predators was fairly constant from year to year and was usually a small fraction of the potential egg deposition. Most deaths occurred between spawning and fry emergence. Hunter's data showed that over a 10-year period, 69–94 percent of the eggs potentially available for deposition were lost before emergence of fry.

Increased utilization of streams and watersheds by logging, mining, and other multiple-use activities has caused concern about the welfare of salmon. A thorough understanding of the factors causing mortality in spawning beds will be required to evaluate the effects of multiple-use activities on pink and chum salmon.

In 1956 the Bureau of Commercial Fisheries gave Saltonstall-Kennedy Act funds to the Fisheries Research Institute (FRI), University of Washington, to study the effects of logging on pink salmon streams in Alaska. These studies concentrated on identifying the time and magnitude of mortality and determining the factors responsible. This paper reviews past work on factors causing mortality in spawning beds and reports findings of field studies in three Southeastern Alaska spawning streams. Field observations on mortality and associated environmental factors thought to cause mortality are described.

REVIEW OF ENVIRONMENTAL REQUIREMENTS OF EGGS AND LARVAE

Given an environment free of mechanical disturbances, the growth, development, and survival of salmon eggs and larvae depend largely upon physical and chemical characteristics of the surrounding water. Properties of water that affect eggs and larvae include temperature, dissolved oxygen content, velocity, mineral and waste metabolite content, and osmotic pressure.

The spawning bed environment is greatly influenced by weather and characteristics of the streambed, stream, and watershed. The quality of intragravel water[3] is influenced in part by the hydrological regimen. Environmental changes within spawning beds can accompany changes in tide level, precipitation, and air temperature. Periods of spawning and development very likely coincide with the seasonal conditions that offer maximum opportunity for survival of the young salmon.

SOURCES OF INTRAGRAVEL WATER

To survive, eggs and larvae must receive an ample supply of oxygenated water suitable in temperature and free of toxic substances. The source of intragravel water may govern to a large extent its physical properties and its suitability for eggs and larvae.

Ground water and surface stream water are the two primary sources of intragravel water. In spawning beds of pink and chum salmon, surface stream water is the primary source of intragravel water (Sheridan, 1962a), while in spring-fed spawning beds commonly used by other salmonid species; e.g., sockeye salmon, ground water may be an important source of intragravel water.

Vaux (1961, 1962) showed that interchange between stream and intragravel water occurred when certain hydraulic requirements of the stream and streambed were satisfied. He formulated models which showed the direction of interchange depends on the curvature of the gravel surface profile. Where the profile was concave, water upwelled; where it was convex, a downdraft occurred. In the absence of curvature, there was no interchange, provided permeability and gravel bed depth did not vary. Vaux verified these relations with field and laboratory experiments. Figure 1 illustrates the direction of interchange with change in curvature of the stream bottom.

WATER TEMPERATURE

Water temperature controls the rate of growth and the developmental and metabolic processes of the salmon embryo. It also affects other water quality characteristics, such as dissolved oxygen concentration.

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[3] The term "intragravel water" refers to water occupying interstitial spaces within the streambed.

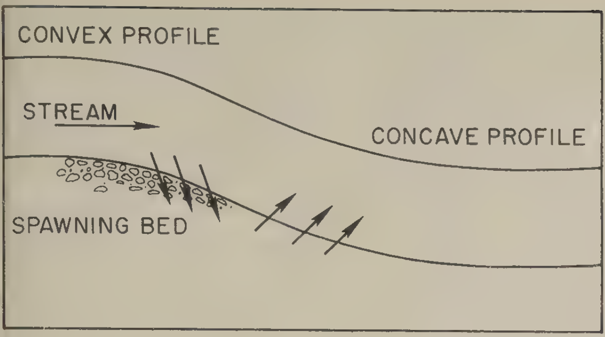

Figure 1.—Changes in direction of interchange with changes in curvature of the stream bottom (from Vaux, 1962). Arrows indicate direction of interchange.

The temperature of intragravel water in pink salmon spawning beds is controlled largely by stream water temperature. Sheridan (1961) obtained a linear correlation coefficient of 0.99 when he related intragravel and stream water temperatures.

Pink and chum salmon embryos and larvae survive in streams where water temperatures drop to 0° C. James (1956) reported water temperatures slightly below 0° C. in pink and chum salmon spawning streams. In an experiment with pink salmon embryos, Combs and Burrows (1957) varied water temperature to coincide with variations observed in Sashin Creek, Southeastern Alaska. They found that embryos reared at 5.5° C. for 30 days and then at 0.5° C. to hatching had almost no mortality.

Information is lacking on tolerance of pink and chum salmon eggs and larvae to high temperature, but studies with other salmonid species suggest that temperatures of 15° C. or higher may be tolerated. Chinook salmon embryos exposed to 20° C. water died at all developmental stages, while embryos exposed to 17° C. water died only at hatching (Donaldson, 1955). Larvae of Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*, survived 16 days in 20° C. water (Bishai, 1960).

Pink and chum salmon normally spawn on declining water temperature after maximum summer temperatures. Sheridan (1962b) reported that pink salmon typically spawned in Southeastern Alaska streams after water temperatures declined to 10° C. or less in late summer. Mean water temperature in Hook Nose Creek was reported to be 12° C. or less when pink and chum salmon spawned (Hunter, 1959). It would appear, therefore, that high temperature seldom exerts a direct lethal stress on pink and chum salmon eggs and larvae.

DISSOLVED OXYGEN SUPPLY

Oxygen is transported to the embryo by diffusion. After water hardening, the capsule of a newly fertilized egg is permeable to oxygen molecules but impermeable to water molecules (Krogh and Ussing, 1937).

The oxygen consumption rate per unit mass of embryonic tissue appears fairly constant over most of the developmental period. During the last two-thirds of the period, the oxygen consumption per gram of embryo remained almost constant for Atlantic salmon (Hays, Wilmot, and Livingstone, 1951). The rate of oxygen consumption for chum salmon was highest but variable during the first one-third of the developmental period and fairly constant thereafter (Alderdice, Wickett, and Brett, 1958).

The rate at which oxygen is consumed by salmon embryos decreases with decreasing dissolved oxygen content of the water below a certain "limiting level" while at dissolved oxygen levels higher than the limiting level, the rate is independent of pressure or content of dissolved oxygen. The limiting level corresponds to the dissolved oxygen content or partial pressure below which normal metabolic functions are affected. There is evidence, also, that the limiting level may vary in a complex manner with temperature and stage of development (Lindroth, 1942; Hays, Wilmot, and Livingstone, 1951).

Alderdice, Wickett, and Brett (1958) calculated theoretical values of the limiting dissolved oxygen level for chum salmon embryos by using an equation originated by Harvey (1928) and later modified by Krogh (1941). The equation is

$$C_0=\frac{SRT}{3U} \tag{1}$$

where C_0=limiting level of oxygen dissolved in the external medium in atmospheres

R=radius of the egg in cm.

S=ml. of oxygen consumed/g. of embryo/minute.

T=thickness of the capsule in cm.

U=diffusion coefficient of oxygen through the capsule in ml. O_2/cm.^{2} of surface/cm. of thickness/minute.

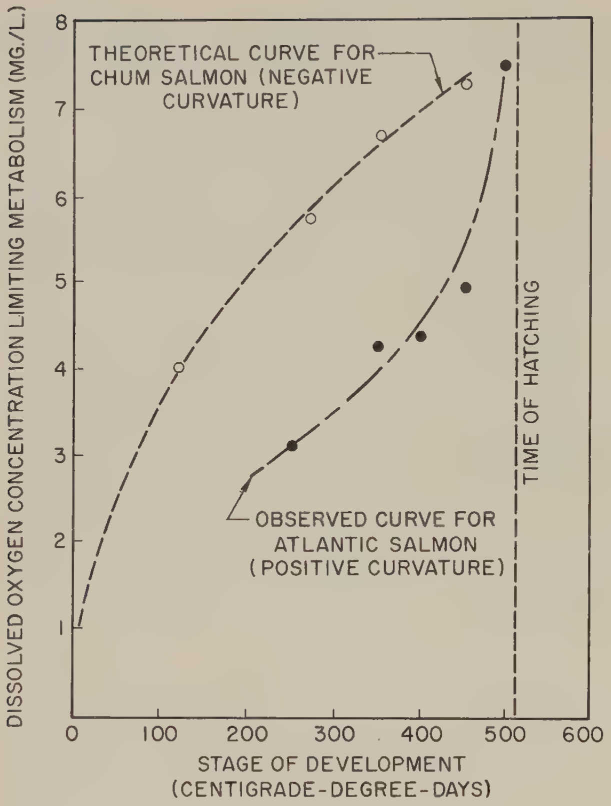

Figure 2.—Concentration of dissolved oxygen first reducing rate of oxygen consumption by salmon embryos. Upper curve is from Alderdice et al. (1958). Lower curve is from Hays et al. (1951). Water temperature is taken to be 10° C., and a centigrade-degree-day is equivalent to a constant temperature of 1° C. above 0° C. over a 24-hour period.

In figure 2, the theoretical values of C_0 at 10° C. obtained for chum salmon by Alderdice et al. (1958) (upper curve) are compared with limiting levels determined experimentally for Atlantic salmon by Hays et al. (1951). The most striking difference between theoretical and observed limiting dissolved oxygen concentrations is the sign of curvature of the connected points. It is doubtful if difference in species would account for positive curvature in Atlantic salmon and negative curvature in chum salmon. The validity of equation (1) as it applies to salmonid embryos is, therefore, questioned.

Wickett (1954) pointed out that the delivery rate of oxygen to an egg or a larva is a function of water velocity as well as oxygen content. Others (Coble, 1961; Shumway, 1960; Silver, 1960; Silver, Warren, and Doudoroff, 1963) gave experimental evidence that variations in velocity affected embryonic growth, development, and survival in much the same manner as variations in oxygen content.

According to curves of figure 2, embryos are most susceptible to low dissolved oxygen levels near the time of hatching. Evidence of this was presented by Hays and Armstrong (1942) and Garside (1959), who observed high mortality at hatching. Because mortality increased with slight increases in temperature, these authors attributed death to an inadequate amount of dissolved oxygen diffusing through the egg capsule.

The effect of oxygen supply rate on growth, development, and survival of salmonid embryos has been investigated by several workers. The dissolved oxygen level causing 50-percent mortality of chum salmon embryos increased from about 0.4 mg./1. at fertilization to 1.4 mg./1. at hatching, when apparent velocity [4] and temperature were maintained at 85 cm./hour and 10° C. (Alderdice et al., 1958). Coho salmon eggs incubated at near true velocity of 3 cm./hour, a temperature of 9° C., and an oxygen level of 2.4 mg./1. survived to hatch but produced larvae about one-third the volume of controls (Shumway, 1960). Similar findings were reported by Silver, Warren, and Doudoroff (1963), who experimented with chinook salmon and rainbow trout, *Salmo gairdneri*, embryos. At near true velocity of 6 cm./hour and a dissolved oxygen content of 2.6 mg./1., Silver (1960) observed abnormal development. At similar low levels of dissolved oxygen, Alderdice et al. (1958) and Garside (1959) described abnormal development of caudal regions during somite formation. Garside also found that the development rate was retarded significantly by reduced oxygen level.

Larvae are more tolerant of low dissolved oxygen levels than are embryos. For Atlantic salmon, Hays et al. (1951) found the dissolved oxygen concentration limiting metabolism of embryos to be 7.5 mg./1. at 10° C. After the eggs hatched the limiting concentration decreased to 4.5 mg./1. Initiation of active respiration across gill membranes having vastly increased respiratory areas may have caused the sudden decrease in limiting oxygen concentration.

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[4] Apparent velocity is measured by dividing the rate of flow by the cross-sectional area of the bed through which the water had passed. The actual or true velocity is greater than the apparent velocity where part of the cross-sectional area is occupied by eggs or other objects.

Several general conclusions may be drawn regarding the dissolved oxygen requirements of pink and chum salmon embryos and larvae. First, the supply of dissolved oxygen made available to an embryo or larva is both a function of dissolved oxygen content and flow velocity of intragravel water. Second, the rate of oxygen consumption per unit mass of embryonic tissue is little affected by growth over most of the developmental period up to hatching. Hence, the rate of oxygen consumption by a population of embryos is possibly a simple function of the biomass present. Third, oxygen levels limiting metabolic processes and causing mortality approach a maximum shortly before hatching. After hatching, there is a sharp decline in limiting levels of dissolved oxygen. By considering only the requirements of eggs and larvae and neglecting changes in the environment, it would appear that the dissolved oxygen requirements of eggs become most critical at hatching.

METABOLIC WASTE PRODUCTS

Two metabolic waste products excreted by salmon eggs and larvae are free carbon dioxide and ammonia. Both are toxic to aquatic organisms.

The effect of free carbon dioxide on the physiology of blood has been studied exhaustively. Jacobs (1920) showed that molecules of free carbon dioxide passed readily through living cell membranes. The ability of eggs and larvae to respire is influenced by the blood's affinity for oxygen, and there is a loss of affinity for oxygen in the presence of free carbon dioxide (Bohr effect). Salmonid blood in vitro lost half of its oxygen-combining capacity in the presence of 150 mg./l. of free carbon dioxide at 15° C. (Irving, Black, and Safford, 1941). Since the oxygen tension equal to one-half saturation is considered to be the minimum compatible with exchange of oxygen to the tissues, a salmonid having its blood oxygen-combining capacity reduced 50 percent would die theoretically of suffocation.

Only a few investigators have investigated the effect of free carbon dioxide on salmonid eggs and larvae. Bishai (1962) induced a marked metabolic stress on Atlantic salmon and brown trout larvae by subjecting them to high free carbon dioxide levels. High mortality among trout embryos occurred at free carbon dioxide levels between 55 and 80 mg./l. in hatchery water (Surber, 1935). Increased mortality of chum salmon embryos was caused by 125 mg./l. of free carbon dioxide (Alderdice and Wickett, 1958). Additional information on the effect of high free carbon dioxide content in conjunction with low dissolved oxygen levels on growth, development, and survival of salmon eggs and larvae will be required before relationships observed between mortality and quality of intragravel water can be fully evaluated.

Ammonia is the most toxic metabolite. Ammonia excreted by salmon eggs and larvae is removed by the surrounding water, but it is possible that toxic concentrations of ammonia occur where the density of eggs and larvae is high and the circulation of intragravel water is poor.

The toxicity of ammonia is related directly to the concentration of free ammonia (NH_3) or non-ionized ammonium hydroxide ($NH_3 \cdot H_2O$) in solution. Ionization of $NH_3 \cdot H_2O$ occurs according to the equilibrium equation

$$NH_3 \cdot H_2O \rightleftarrows NH_4^+ + OH^-$$

Ionization is nearly complete at pH 7.0 and lower, and ammonia is least toxic in waters having high concentrations of hydrogen ions (pH $<$7.0). Formation of carbonic acid from respired free carbon dioxide would, therefore, tend to decrease the toxicity of ammonia.

Reviews of influence of ammonia on fish have been given by Doudoroff and Katz (1950) and Doudoroff (1957). These authors concluded that additions of 2 to 7 mg./l. of ammonia to natural waters could kill fish. Experiments by Wuhrmann and Woker (1948) showed that concentrations of only 1.2 mg./l. of NH_3 were lethal to fresh-water fish of the genus *Squalius*. They also found that 1.3 mg./l. of NH_3 killed rainbow trout fry.

According to Wolf (1957a, 1957b), blue-sac disease was induced by subjecting salmonid embryos to high concentrations of ammonia. The incidence of disease was roughly proportional to the contact period and the NH_3 concentration.

SALINITY

Pink and chum salmon spawn in intertidal areas of streams, and in some streams more fry are produced in intertidal areas than in upstream areas (Kirkwood, 1962). From field observation alone, it is apparent that pink and chum salmon eggs and larvae can tolerate intermittent high salinity.

Rockwell (1956) exposed pink and chum salmon eggs and larvae to constant high salinity and found no evidence that fertilization of eggs was affected by salinities up to 18°/oo. The tolerance of embryos to sea water was a function of osmotic pressure, time of exposure, and stage of development. Mortality was attributed to dehydration. He found a marked reduction in the rate of early growth of chum salmon embryos at constant salinities of 12°/oo and greater and a total mortality to hatching at a salinity of 12°/oo. At 6°/oo salinity, survival to hatching was less than that in the controls.

Larvae are more tolerant of high salinity than eggs. According to Rockwell (1956), salinities as high as 18°/oo killed few pink salmon larvae. Chum salmon larvae were less tolerant, some dying at a salinity of 12°/oo.

Salinity of intragravel water in pink and chum salmon intertidal spawning beds is influenced markedly by tidal action. Hanavan and Skud (1954) found salinity of intragravel water of pink salmon spawning beds corresponds closely to salinity of overlying water. Also, they observed high survival of pink salmon eggs and larvae where tidal inundation prevailed during 35 percent of the incubation period. Ahnell (1961) observed that the salinity of intragravel water remained high for a period after the tide had receded and after fresh water had flowed over the streambed. He found also that high salinity of intragravel water was frequently associated with low dissolved oxygen concentration.

The effect of salinity on pink and chum salmon fry production is still poorly understood, although highly productive spawning areas exist in intertidal zones of streams (Kirkwood, 1962). Eggs and larvae of both species can tolerate intermittent high salinity, but tolerance levels have not yet been defined. Also, the retention of salt water by spawning beds and the influence of salt water on temperature, oxygen levels, and water velocity have not been studied in detail. The ultimate need is to determine the relative potential of intertidal and upstream areas to produce fry.

PERMEABILITY OF BOTTOM MATERIALS

It has already been pointed out that the oxygen delivery rate to an egg or larva is a function of both the oxygen content and velocity of intragravel water. Apparent velocity of water flowing within the streambed can be described by the equation.

$$v=\eta i \tag{2}$$

Where v=apparent velocity,
η=permeability coefficient, and
i=hydraulic gradient.

According to this equation, apparent velocity of intragravel water varies directly with the permeability of materials through which it passes. Other factors being equal, the permeability of bottom materials in spawning beds should be directly related to their potential to produce salmon fry; Wickett (1958) gave evidence that the average survival of pink and chum salmon eggs and larvae in four British Columbia streams was directly related to the permeability of bottom materials (fig. 3).

The permeability of bottom materials is a function of particle compaction, arrangement, and size. McNeil and Ahnell (1964) showed that the permeability of bottom materials in a pink salmon spawning bed is inversely related to the fraction of fine particles composing the total volume of the bed. Thus, the resistance to flow caused by the presence of fine particles in salmon spawning beds must govern, to a large extent, their potential to produce healthy fry.

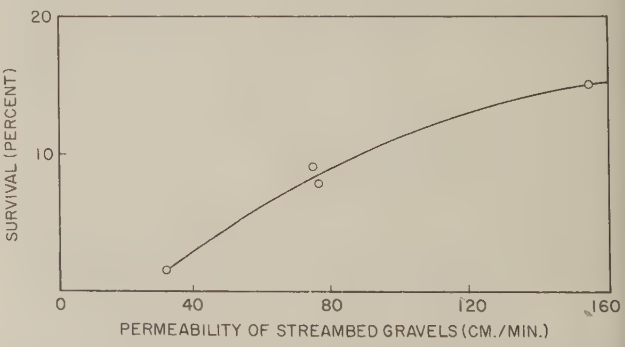


Figure 3.—Observed relation reported by Wickett (1958) between permeability and survival of pink and chum salmon to migrant fry.

STABILITY OF SPAWNING BEDS

Dislodgment of salmonid eggs and larvae from spawning beds during high water has been described by a number of workers (Hobbs, 1937; Hutchinson and Shuman, 1942; Davidson and Hutchinson, 1943; Withler, 1952; Needham and Jones, 1959; Wickett, 1959). Estimates of mortality rates from gravel movement have not been made in most instances. Furthermore, little is known about the interactions of factors creating unstable conditions in spawning beds and causing mortality rates to increase.

Changes in surface profile occur where a streambed degrades or aggrades. It is possible, however, for bed movement to occur without an associated change in surface profile or gradient (Mackin, 1948). One important unsolved problem is to determine if bed movement can cause appreciable mortality where there is no associated change in streambed gradient.

The effect of the pool-riffle complex on the capacity of streams to produce pink and chum salmon is not yet well understood. Factors important in generating the pool-riffle complex include debris in the high-flow channel (Bishop and Shapley, 1963) and bends in the channel. Shifts in position of debris create unstable conditions in the spawning bed which could lead to dislodgment of salmon eggs and larvae.

METHODS

STUDY STREAMS

Field studies described in this report were conducted mostly in three streams located in the Kasaan Bay region of Prince of Wales Island, Southeastern Alaska: Harris River, Indian Creek, and Twelvemile Creek (fig. 4). Watersheds of the study streams are precipitous. Soils are shallow and underlaid with impermeable materials. Except for muskegs, which are poorly drained areas, the watersheds have a very low capacity to retain water. Runoff is rapid, and peak discharges occur within a few hours after the beginning of heavy rainfall. These high discharges occur mostly in autumn.

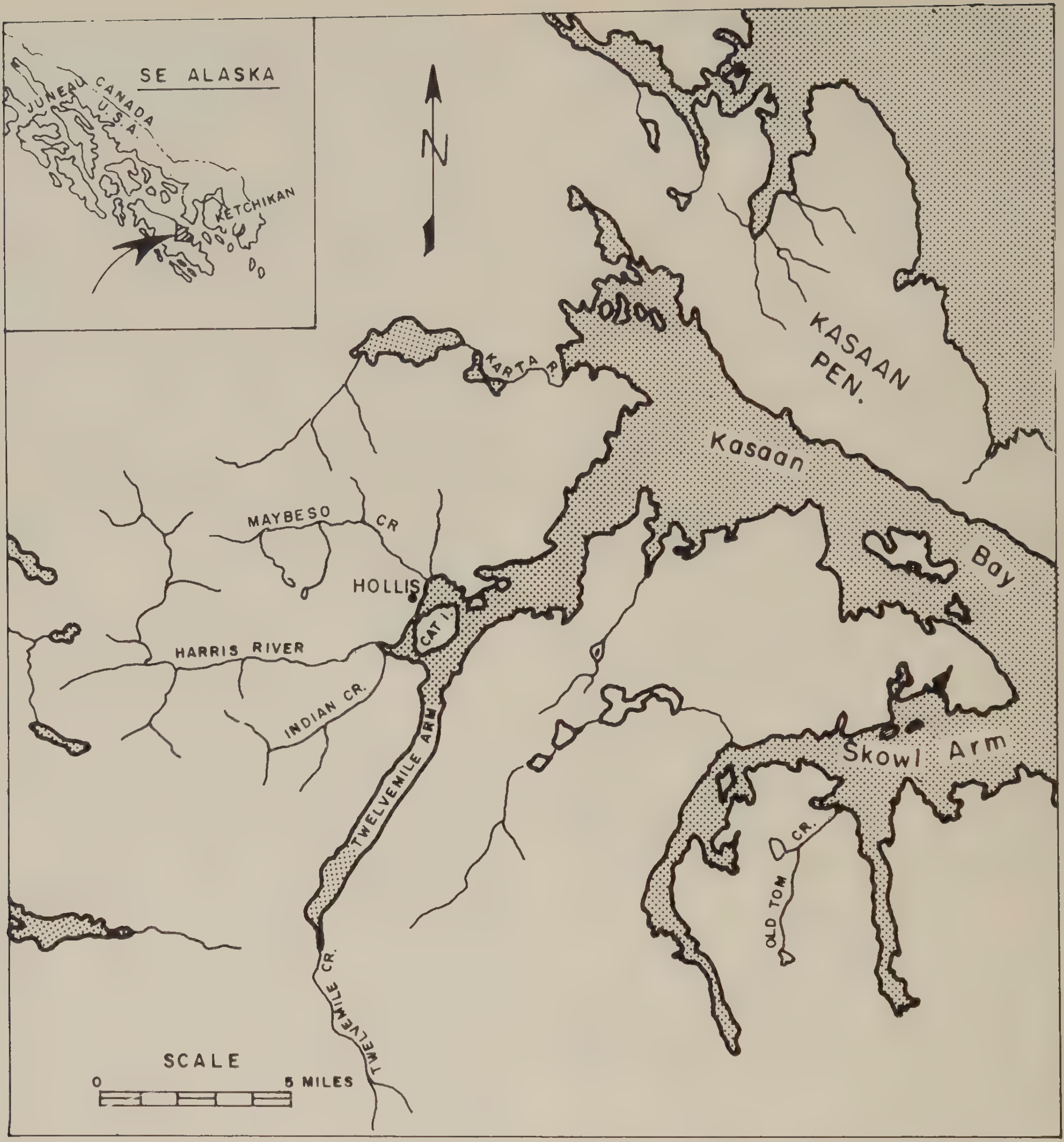
The study streams occasionally freeze over in winter, when water temperatures near 0° C. have been recorded for as long as 6 consecutive days; summer water temperatures rarely exceed 13° C. (James, 1956).

Adult pink and chum salmon usually enter the study streams to spawn between mid-August and late September. Spawning occurs mostly in September. A large percentage of pink salmon spawn in intertidal areas, where the density of spawners is highest in most years.

Harris River is the largest of the three study streams. Salmon have access to about an 8-mile section of the main stream and its North Fork. Chum salmon were observed to spawn mostly in the North Fork, but pink salmon exhibited a marked preference for a ½-mile section of the upper intertidal zone. Discharge during the spawning period commonly fluctuates between 22 and 1,800 cubic feet per second (c.f.s.). During autumn storms, average daily discharge may approach 5,000 c.f.s. Width of intertidal spawning riffles during low flow averages about 60 feet. Spawning beds consist of materials mostly less than 4 inches in diameter.

Indian Creek is the smallest of the study streams but exhibits pronounced fluctuations in discharge. During the spawning period, discharge commonly varies between 4 and 300 c.f.s. Average daily discharge during autumn storms approaches 900 c.f.s. some years, and a peak instantaneous discharge of 6,400 c.f.s. was recorded on one occasion (McNeil, Shapley, and Bevan, 1962). Pink salmon spawn in Indian Creek, primarily in an intertidal section one-fourth mile long beginning at the confluence with Harris River. The average width of Indian Creek spawning beds at low flow is about 25 feet. Spawning beds consist of materials mostly less than 6 inches in diameter.

Twelvemile Creek has a more stable discharge than either Harris River or Indian Creek. During spawning, average daily discharge usually varies between 12 and 300 c.f.s. During autumn storms, average daily discharge rarely exceeds 600 c.f.s. Intertidal spawning areas average about 45 feet wide during low flow, and spawning beds consist mostly of materials less than 4 inches in diameter, and contain a high percentage of sand and silt. About 5 miles are believed accessible to salmon, but the distance has not been measured. Heaviest densities of spawning pink salmon have been observed in the intertidal zone. Chum salmon, less abundant here than pink salmon, commonly spawn in the intertidal zone, too.


SE ALASKA
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HOLLIS
CAT I.
HARRIS RIVER
INDIAN CR.
TWELVEMILE ARM
Skowl Arm
OLD TOM CR.
TWELVEMILE CR.
SCALE
0
5 MILES

Figure 4.—Locations of study streams (Harris River and Indian and Twelvemile Creeks) in the Kasaan Bay region of Prince of Wales Island, Southeastern Alaska.

Field studies began in 1956 when FRI personnel selected six spawning riffles ranging in area from 260 to 650 m.^{2} for sampling. Spawning riffles were sampled in 1956, 1957, and 1958 to measure mortality of eggs and larvae and the quality of intragravel water (table 1).

The study areas were enlarged in 1958, when FRI personnel selected five spawning areas ranging in size from 3,400 to 13,400 m.^{2} The areas included major spawning grounds of pink and chum salmon in Harris River and Indian and Twelvemile Creeks and incorporated the six spawning riffles previously sampled. The sampling areas were selected to represent both intertidal and upstream areas of the study streams (table 1). Factors measured included density

TABLE 1.—*Size and location of six spawning riffles sampled in 1956, 1957, and 1958 and five spawning areas sampled in 1958, 1959, and 1960*

Study area and years sampled	Tide level	Area
1956, 1957, 1958	*Meters*	*Meters*
Riffle A, Harris River	3. 4	305
Riffle B, Indian Creek	4. 0	386
Riffle C, Indian Creek	5. 2	260
Riffle D, Twelvemile Creek	3. 7	648
Riffle E, Twelvemile Creek	4. 3	372
Riffle F, Twelvemile Creek	4. 9	486
1958, 1959, 1960		
Intertidal Harris River	3. 7–4. 3	7, 800
Upstream Harris River	----------	13, 400
Intertidal Indian Creek	3. 4–5. 2	3, 400
Intertidal Twelvemile Creek	3. 7–4. 9	5, 580
Upstream Twelvemile Creek	----------	6, 130

and distribution of spawners, mortality of eggs and larvae, quality of spawning beds, and quality of intragravel water.

To insure random sampling, FRI personnel drew maps of areas sampled to scale on cross-sectional paper having 100 squares per square inch. The scale selected made each square representative of not more than a 0.4 m.^{2} area in the stream. Co-ordinate axes were established for each map, and sampling points were selected by the following procedure. A pair of random numbers was obtained from a random number table—one number for the abscissa and the other number for the ordinate. Distance of the selected square from a reference point and an angle of the selected square from a reference line were measured on the map and recorded for use in the field. When a sample was to be taken, the angle and distance of the sample area were measured from the base line and reference point.

MEASUREMENT OF ENVIRONMENTAL FACTORS

The Northern Forest Experiment Station, U.S. Forest Service, operated a weather station at Hollis, a logging community located within 3 miles of Harris River and Indian Creek spawning areas and within 12 miles of Twelvemile Creek spawning areas (see fig. 4). Forest Service personnel obtained continuous records of air temperature and precipitation during the study. Instruments installed and operated by the Northern Forest Experiment Station recorded water level and temperature of each study stream. Forest Service personnel also established discharge rating curves for each stream. James (1956) gives further information on hydrological studies made by the Forest Service.

Physical quality of the spawning bed was evaluated in each area where observations were made on egg and larval mortality. Environmental attributes measured included the dissolved oxygen content of intragravel water and the size composition and permeability of bottom materials. McNeil (1962b) described the techniques used to measure dissolved oxygen levels and McNeil and Ahnell (1964) described the methods of measuring size composition and indexing permeability of bottom materials.

ESTIMATION OF SPAWNING DENSITY AND POTENTIAL EGG DEPOSITION

Fisheries Research Institute (FRI) personnel estimated the number of female pink and chum salmon occupying study areas by means of daily foot survey censuses when water conditions permitted. Institute personnel also observed tagged females daily to estimate average life on the spawning ground (redd life). Females were tagged before they entered the spawning ground and FRI workers calculated the total number spawning by summing daily abundance and dividing by average redd life; i.e.,

$$\text{Number spawning} = \frac{\sum \text{daily abundance in female days}}{\text{average redd life in days}}$$

A summation of daily abundance was obtained by constructing an eye-fitted curve of the daily counts of females and determining the area under the curve in female days. In the determination of average redd life, daily observations on tagged females have been adjusted to account for the periodicity of observations. Assuming that each tagged female occupied the spawning bed one-half day before being observed the first time and one-half day beyond the date of the last observation, I added 1 day to the duration each tagged female was observed.

Two observers made most of the survey censuses; periodic comparisons of their counts showed consistently good agreement. Although it was not feasible to determine bias in estimates, a recent unpublished study conducted by the author at Sashin Creek revealed good agreement between the number of spawning female pink salmon estimated by this method and the number counted into the stream.

COLLECTION OF EGGS AND LARVAE

Eggs and larvae were collected with a hydraulic sampler (McNeil, 1962a) from small enclosed quadrat or circular areas (sampling units) of known area. Area of sampling units varied from 0.2 to 0.9 m.^{2}

Samples preserved in the field were examined later to determine the number of live and dead eggs and alevins collected. Eggs were preserved in a clearing solution (Stockard's solution).

ESTIMATION OF MORTALITY

Data on egg and larval populations were analyzed by three methods to obtain information on temporal changes and spatial differences in mortality levels. Although the methods have been described (McNeil, 1962a), they will be reviewed briefly here.

Ratio of Dead to Total Eggs and Larvae

Mortality has commonly been estimated from ratios of dead to total eggs and larvae collected in k samples; i.e.,[5]

$$\hat{M}_r = \frac{\sum_1^k \frac{\text{dead}}{\text{live}+\text{dead}}}{k} \tag{3}$$

An estimate of mortality based on such ratios underestimates true total mortality where the number of eggs and larvae present in the spawning bed at the time of sampling is less than the number of eggs originally available for deposition. Despite this limitation, estimates of M_r are very helpful in establishing time of mortality where mortality is caused by factors not associated with the direct removal of eggs and larvae from the spawning bed and are sometimes useful in setting lower limits to total mortality.

Actual and Potential Abundance

Total mortality (M_t) can be estimated from statistics on potential egg deposition and abundance of live eggs and larvae at the time of sampling. In this study, estimates of M_t were calculated from the double inequality

$$1-\frac{\bar{a}}{E'} \leq \hat{M}_t \leq 1-\frac{\underline{a}}{E'} \tag{4}$$

In double inequality (4), the value $\bar{a}$ and $\underline{a}$ are the upper and lower confidence limits respectively of the estimated number of live eggs and larvae per m.^{2} of spawning bed, and E′ is the expected number per m.^{2} Values for $\bar{a}$ and $\underline{a}$ were calculated with the standard error of the mean obtained from either arithmetic or log-transformed counts of live eggs and larvae. Log-transformed counts are used only if the efficiency of the estimate of M_t is increased without introducing significant bias.

Where the logarithmic transformation is used, each observed count is transformed by the equation

$$b_i = \log_{10}(n_i + \beta) \tag{5}$$

In equation (5), b_i is the transformed variate and n_i is the number of live eggs and larvae collected at the i^{th} point. The term β is a constant which describes the degree of contagion in a negative binomial distribution. A value of β is calculated from the expected frequency of zero observations in a negative binomial distribution. The method, described by Anscombe (1949) and Bliss (1953), requires an iterative solution of the equation

$$\frac{1}{\beta}\log_{10}(1+\beta\bar{n}) = \log_{10}\left(\frac{k}{k'}\right), \tag{6}$$

where k is the total number of observations, k' is the number of zero observations, and $\bar{n}$ is the sample arithmetic mean.

To set confidence limits to estimates of abundance of eggs and larvae with log-transformed data, the mean log values must be corrected so that the arithmetic mean will result from the antilog. A correction term is required because the mean of log-transformed data is geometric rather than arithmetic (Ricker, 1958, ch. 11). Jones (1956) developed the correction term and described the method used here to calculate confidence limits with log-transformed counts. The equation used to obtain an arithmetic mean ($\bar{n}$) from the log-transformed counts is

$$\bar{n} = \text{antilog}\,(\bar{b} + 1.1518 s_b^2) - \beta, \tag{7}$$

where $\bar{b}$ is the logarithmic mean value and s_b^2 is the sample variance of the log-transformed counts. The term β is subtracted to correct for its addition to the counts before making the transformation in equation (5).

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[5] The value $\hat{M}_r$ estimates the population parameter M_r. The circumflex sign also will be used to identify estimators of other population parameters.

Provided the estimates $\bar{a}$, $\underline{a}$, and E' are unbiased, double inequality (4) gives an unbiased estimate of the total mortality fraction from the time of spawning to the time of sampling. Absence from the spawning bed of dead eggs and larvae does not introduce bias to estimates of M_t as it does to estimates of M_r based on ratios of dead to total eggs and larvae present.

Potential egg deposition (E) is calculated by multiplying the estimated number of female salmon spawning within each area by average fecundity. The value E' is obtained by multiplying E by a factor correcting for the fraction of eggs and larvae present within the streambed actually collected. In the present study, the relationship

$$E' = \frac{9}{10} E \tag{8}$$

is used. Methods used to obtain the correction term, $\frac{9}{10}$ are described elsewhere (McNeil' 1962a).

More recent studies provide evidence that estimates of M_t obtained with a hydraulic sampler are fairly representative of the true total mortality fraction. I used a hydraulic sampler to estimate total mortality of 1961 and 1963 brood year preemergent pink and chum salmon fry in Sashin Creek, where total fresh-water mortality also was calculated from weir counts of adults entering and fry leaving the stream. In Sashin Creek, it was assumed that $E' = \frac{93}{100} E$ for purposes of setting confidence limits to M_t. Based on samples of preemergent fry obtained with a hydraulic sampler, confidence limits of M_t bracketed the total mortality fraction calculated for each species and brood year from weir counts. In each instance, mean estimated mortality from sampling preemergent fry and from counting migrant fry differed by less than 2 percent. The results are summarized in table 2. In Sashin Creek, potential egg deposition was determined by counting adults entering the stream. In Harris River and Indian and Twelvemile Creeks, the methods of estimating potential egg deposition were not as precise, and it is doubtful if estimates of M_t were completely unbiased.

TABLE 2.—*Total mortality of Sashin Creek pink and chum salmon estimated by sampling preemergent fry with hydraulic sampler and by counting migrating fry at weir*

Species and brood year [1]	Mortality estimated by sampling preemergent fry		Mortality estimated by counting migrating fry
	Mean	90-percent confidence limits of the mean	
Pink salmon			
1961	0.777	±0.041	0.790
1963	.800	±.052	.804
Chum salmon			
1961	.928	±.056	.917
1963	.997	±.040	.995

[1] Mortality of the 1962 brood year was not estimated by sampling preemergent fry because populations were very small. Only 4 pink and 42 chum salmon females entered Sashin Creek to spawn in 1962.

Presence or Absence of Eggs and Larvae

Estimates of the population parameters M_r and M_t sometimes fail to differ significantly when other evidence suggests high mortality. A chi-square test helped demonstrate significant mortality in certain of these cases and often proved to be a more sensitive test for detecting time of mortality than the mortality estimates M_t and M_r.

The chi-square test is based on the premise that the proportion of points within a spawning bed occupied by live eggs and larvae varies with total mortality. If no change in mortality occurs, the following conditions will be satisfied: (1) There will be no decrease in the expected fraction of points populated by eggs or larvae (live plus dead); (2) there will be no decrease in the expected fraction of points populated by live eggs and larvae; and (3) there will be no increase in the expected fraction of points populated by dead eggs or larvae.

In this study, each point sampled was classified according to the number of eggs and larvae present, with points containing less than 35 eggs and larvae per m.^{2} (k_0) being classified together. The classes used were (1) less than 35 live plus dead eggs and larvae per m.^{2}, (2) less than 35 live eggs and larvae per m.^{2}, and (3) less than 35 dead eggs and larvae per m.^{2}.

Principal purpose of the classification scheme was to classify jointly all points containing few eggs and larvae and those containing none. The selection of less than 35 per m.^{2} for joint classification was arbitrary, however.

I tested each class independently with chi-square (see Snedecor, 1956), and set confidence limits to the number of points estimated to contain fewer than 35 eggs and larvae per m.^{2} from the normal approximation of the binomial distribution.

The 90-percent confidence limits of k_0 ($\underline{k}_0$ and $\bar{k}_0$) are obtained from the expression

$$(\bar{k}_0, \underline{k}_0) = k\hat{p}_0 \pm 1.645[k\hat{p}_0\ (1-\hat{p}_0)]^{1/2} \qquad (9)$$

where k is the number of points sampled and $\hat{p}$ is the fraction of points estimated to contain fewer than 35 eggs and larvae per m.[2]

OBSERVATIONS ON ENVIRONMENT AND MORTALITY

Although numerous workers have postulated factors causing mortality of eggs and larvae, few have presented quantitative estimates of mortality satisfying three essential criteria: (1) Estimates free of bias, (2) estimates representative of natural populations, and (3) estimates related directly to causative factors. It is not surprising that these criteria have not been met entirely in field studies, for there are many difficult problems requiring solution. In the present study, an effort was made to reduce (or at least recognize) bias in mortality estimates. Furthermore, because of the randomization techniques used, the samples were thought to be representative of the populations studied. However, the difficulties in associating observed mortality levels with their causative factors are formidable even with the first two criteria being satisfied in part. The problem of relating observed mortality levels to causative factors is complicated in most instances because of interactions among environmental factors.

I attempted to account for interactions by classifying environmental factors causing mortality into generally inclusive groupings: (1) Oxygen supply and related factors, (2) stability of the spawning bed, and (3) freezing of intragravel water. I did not consider one inclusive grouping—pathogenic agents.

OXYGEN SUPPLY AND MORTALITY

Environmental requirements of salmon eggs and larvae were briefly reviewed in an earlier section. My purpose here will be (1) to describe the physical characteristics of spawning beds where observations on mortality were made, and (2) to describe the relation between environmental quality (as related to oxygen supply) and the observed mortality levels.

Dissolved Oxygen Content of Intragravel Water

The dissolved oxygen content of intragravel water was consistently lower at the beginning than at the end of the spawning period in all study streams. There also were observed spatial differences in mean dissolved oxygen levels among and within the study streams.

In late August, at the beginning of spawning, oxygen levels appeared to be lowest in the intertidal Harris River and the upstream Twelvemile Creek spawning areas and highest in the upstream Harris River and the intertidal Indian Creek and Twelvemile Creek spawning areas. Near the end of spawning, in late September, differences in mean oxygen levels were no longer significant among the spawning areas sampled. The data are summarized in table 3, and mean values obtained in 1959 are shown in figure 5 to illustrate the kind of relation observed.

Differences among years in mean dissolved oxygen levels were considerably greater than differences among streams. Summer 1957 was of particular interest in this regard because unusually low levels of dissolved oxygen were observed. Average values of all dissolved oxygen determinations made in the study streams near the beginning of spawning over the period 1956

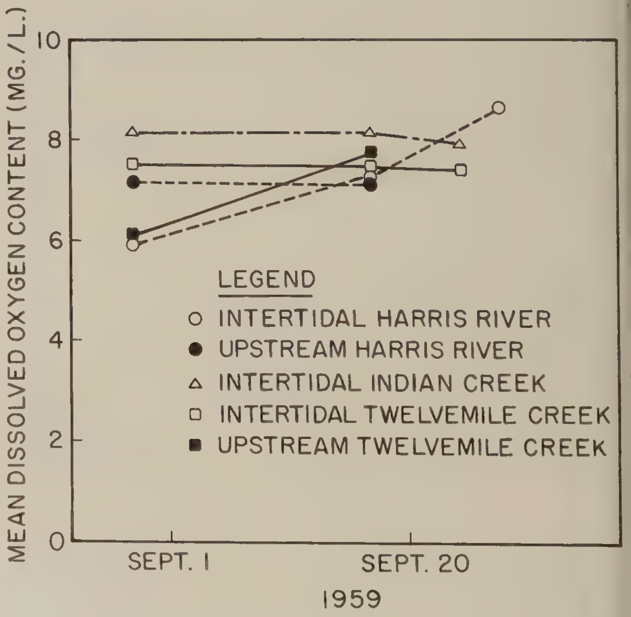

FIGURE 5.—Mean dissolved oxygen content of intragravel water in the study streams over the period of spawning in 1959.

TABLE 3.—*Ninty-five-percent confidence interval estimates of mean dissolved oxygen content of intragravel water in study streams*

[Water samples were collected 7 to 10 inches beneath the streambed surface. All values are given as mg./l.]

Date	Harris River		Indian Creek Intertidal	Twelvemile Creek	
	Intertidal	Upstream		Intertidal	Upstream
1958					
ept. 1				$6.3<\mu<7.4$	$4.8<\mu<6.1$
Nov. 30				$8.3<\mu<9.5$	$8.0<\mu<9.6$
1959					
ug. 28	$5.1<\mu<7.0$	$6.4<\mu<8.1$	$7.5<\mu<8.9$	$6.8<\mu<8.3$	$5.3<\mu<6.9$
ept. 17	$5.6<\mu<9.1$	$6.0<\mu<8.4$	$7.1<\mu<9.3$	$6.5<\mu<8.5$	$6.7<\mu<8.4$
ept. 24			$7.4<\mu<8.4$		
ept. 27	$8.1<\mu<9.3$				
1960					
ug. 24				$6.8<\mu<8.0$	$5.6<\mu<6.7$
ug. 25	$5.4<\mu<6.6$	$5.8<\mu<7.0$	$6.3<\mu<7.8$		
ept. 14	$7.1<\mu<9.0$		$7.6<\mu<8.9$	$7.5<\mu<9.0$	$5.4<\mu<7.2$

hrough 1960 are shown in figure 6. Oxygen levels were severely depressed in 1957, and high mortality of 1957 brood year eggs occurred. The relation between mortality and oxygen levels will be discussed later.

COMPOSITION OF BOTTOM MATERIALS

There were marked differences in size composition of bottom materials among the study streams. The bed of Indian Creek contained greater quantities of coarse materials and smaller quantities of fine materials than the beds of either Harris River or Twelvemile Creek. The bed of Twelvemile Creek contained considerably more silt than the beds of Indian Creek or Harris River. Table 4 lists the average size composition (by volume) of bottom materials in each of the study streams.

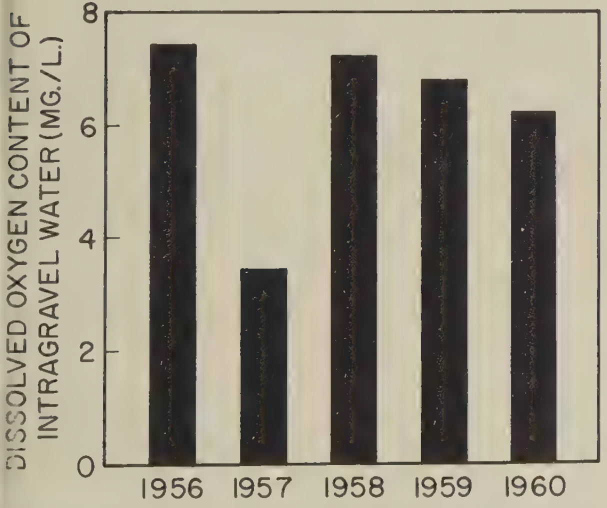

FIGURE 6.—Approximate mean dissolved oxygen content of intragravel water in the three study streams (Harris River, Indian Creek, and Twelvemile Creek) near the beginning of the spawning period (1956–60).

The volume of fine materials in salmon spawning beds is inversely related to the permeability of bottom materials (McNeil and Ahnell, 1964). Figure 7 shows the observed relation between the percentage of bottom materials by volume passing through an 0.833-mm. sieve and the coefficient of permeability.

The observed mean percentages of solids passing through an 0.833-mm. sieve are listed below for the study streams in order of decreasing permeability:

	Percent
1. Intertidal Indian Creek	9
2. Upstream Harris River	14
3. Intertidal Harris River	17
4. Intertidal Twelvemile Creek	18
5. Upstream Twelvemile Creek	19

McNeil and Ahnell (1964) found that the finest fractions contained the highest percentages of organic detritus. It will be assumed, therefore,

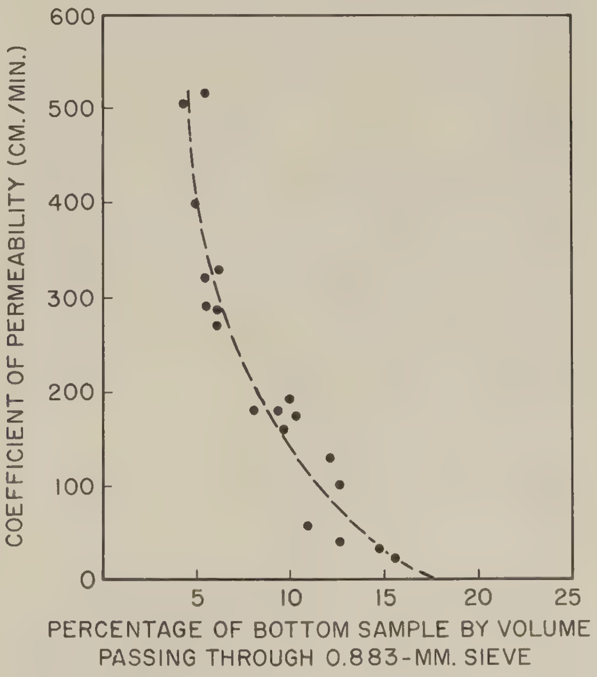

FIGURE 7.—Relation observed between coefficient of permeability and the fraction by volume of a bottom sample passing through an 0.833-mm. sieve (from McNeil and Ahnell, 1964). Curve fitted by eye.

TABLE 4.—*Average size composition of bottom materials in the study streams* [1]

[All rocks larger than 105 mm. diameter have been excluded]

Spawning area	Mean percent of total volume of solids retained by sieves with opening (in mm.) of— [2]									Percent of total volume of solids settling from suspension
	26.26	13.33	6.88	3.33	1.65	0.833	0.417	0.208	0.104	
Harris River (intertidal)	25.1	14.6	13.2	11.0	7.9	11.5	10.5	2.7	0.4	3.1
Harris River (upstream)	24.0	16.2	14.1	11.8	8.4	11.8	9.2	2.4	.4	1.9
Indian Creek (intertidal)	35.2	15.3	12.9	11.3	7.3	8.6	4.9	1.3	.4	2.7
Twelvemile Creek (intertidal)	21.2	15.1	13.9	12.5	8.8	10.7	8.4	2.5	.9	5.9
Twelvemile Creek (upstream)	19.7	13.9	13.0	12.9	9.6	11.6	9.5	3.6	1.2	5.0

[1] For a description of methods of collecting and classifying samples, the reader is referred to McNeil and Ahnell (1964).

[2] Data are taken from table 2 of McNeil and Ahnell (1964).

that the percentage of fine materials obtained from the settling funnel used in the analysis of bottom samples (McNeil and Ahnell, 1964) provides an index of the relative amounts of extraneous organic matter in spawning beds. Percentages of fine materials passing through a 0.104-mm. sieve, observed in the total volume of bottom materials collected from the areas sampled, are listed below in order of increasing values:

	Percent
1. Upstream Harris River	1.9
2. Intertidal Indian Creek	2.7
3. Intertidal Harris River	3.1
4. Upstream Twelvemile Creek	5.0
5. Intertidal Twelvemile Creek	5.9

The rate of interchange between stream and intragravel water is believed to be related to gradient and roughness of the stream bottom. Steep-gradient areas have a greater potential for changes in curvature of the stream bottom than shallow-gradient areas, and coarse materials give greater roughness to the stream bottom than fine materials. To index relative roughness, the study areas are listed below in order of decreasing amounts of solids retained by the largest sieve used in this study (26.26-mm.).

	Percent
1. Intertidal Indian Creek	35
2. Intertidal Harris River	25
3. Upstream Harris River	24
4. Intertidal Twelvemile Creek	21
5. Upstream Twelvemile Creek	20

In addition to having the largest fraction of coarse gravel, Indian Creek also had the steepest gradient (0.7 percent as opposed to 0.2 to 0.4 percent for the other areas). The evidence suggests that the interchange potential of Indian Creek is greater than Harris River or Twelvemile Creek.

Spawning Density

According to the evidence just presented, environmental conditions related to oxygen supply and survival of eggs and larvae would appear to be most favorable in intertidal Indian Creek and least favorable in upstream Twelvemile Creek. The remaining three areas did not appear to vary significantly with regard to the environmental factors evaluated. Observed distributions of spawning female pink and chum salmon appeared to be related to the physical characteristics of the spawning beds studied.

For the years 1958, 1959, and 1960 intertidal Indian Creek had the highest average density of spawners, and upstream Harris River and Twelvemile Creek had the lowest. In order of decreasing average density, the density of spawning females in the sampling areas were estimated to be:

1. Intertidal Indian Creek	mean=35 females per 100 m.^{2} (range 13 to 46 females per 100 m.^{2})
2. Intertidal Harris River	mean=29 females per 100 m.^{2} (range 13 to 48 females per 100 m.^{2})
3. Intertidal Twelvemile Creek	mean=17 females per 100 m.^{2} (range 11 to 25 females per 100 m.^{2})
4. Upstream Harris River	mean=4 females per 100 m.^{2} (range 2 to 6 females per 100 m.^{2})
5. Upstream Twelvemile Creek	mean=4 females per 100 m.^{2} (range 1 to 10 females per 100 m.^{2})

Time and Magnitude of Mortality

The amount of dissolved oxygen required by salmon eggs and larvae for normal metabolism approaches a maximum just before hatching (see fig. 2). After hatching, levels of dissolved oxygen limiting metabolism are greatly reduced, and oxygen requirements are least likely to be satisfied before hatching.

Pink and chum salmon eggs begin to hatch in the study streams in November, and most hatch before mid-December. Figure 8 shows the percentages of live eggs and larvae collected from intertidal Harris River and Indian Creek that had hatched before the date of sampling. Twelvemile Creek is thought to lag 1 or 2 weeks behind Harris River and Indian Creek with regard to time of hatching, because the peak of spawning occurs about 1 week later.

After the spawning period, it is convenient to consider two periods during which mortality occurs—prehatching (autumn) and posthatching (winter). The dissolved oxygen supply and related factors are thought to exert their greatest influence on mortality before hatching, so the discussions here will be limited primarily to mortality of eggs.

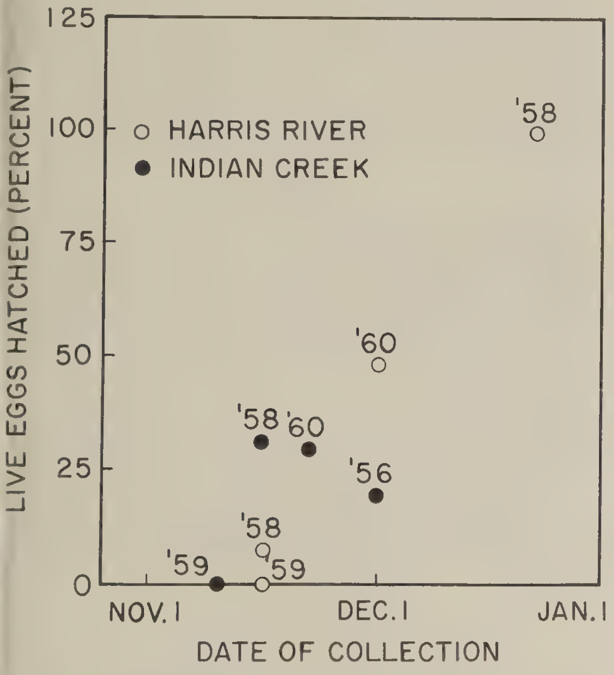

Figure 8.—Percentage of live eggs and larvae in collections from intertidal Harris River and Indian Creek hatching before the date of sampling. (Brood years are indicated by numerals.)

In this study, estimates of three population parameters thought to provide evidence of the effect of oxygen supply and related factors on egg mortality were used: (1) Total mortality fraction (M_t), (2) mortality fraction from ratios of dead eggs in samples (M_r), and (3) fraction of points containing fewer than 35 dead eggs per m.[2] (p_0).

An estimate of M_t includes mortality from all causes, and this estimate includes eggs removed from the spawning bed. Such removal can obscure mortality from causes where there is no direct removal of eggs; therefore, the estimated total mortality ($\hat{M}_t$) was often of limited value in measuring egg mortality from oxygen supply and related factors. Furthermore, estimates of M_t were highly inefficient, and the resulting confidence limits were often broad.

The other two estimates ($\hat{M}_r$ and $\hat{p}_0$) also had limitations imposed by the disappearance of eggs from the spawning bed. Disappearance from gravel shift alone would have little effect on validity of estimates of ratios of dead to total eggs present in the streambed ($\hat{M}_r$), provided live and dead eggs disappear in numbers proportional to their abundance. On the other hand, losses from decomposition and scavenging affect only dead and dying eggs and would cause mortality to be underestimated by $\hat{M}_r$.

Use of the number of points where eggs were present or absent to index occurrence of mortality also would be affected by disappearance because evidence of mortality from factors not related to the direct removal of dead eggs would have been destroyed. Major losses due to gravel shift would tend to invalidate the use of $\hat{p}_0$ to detect significant mortality possibly caused by oxygen supply and related factors.

With these possible limitations in mind, the estimates of M_t, M_r, and p_0 are used to evaluate prehatching mortality of the 1956–60 brood years in the three study streams. Each brood year will be considered separately.

1956 Brood Year

Sampling was confined to spawning riffles A (Harris River), B and C (Indian Creek), and D and E (Twelvemile Creek). Workers sampled the riffles in late November 1956 and in late February

TABLE 5.—*Estimated mortality of 1956 brood year pink and chum salmon eggs and larvae based on ratios of dead to total specimens collected*

Stream [1]	Fraction of dead eggs in late November ($\hat{M}_r$)		Fraction of dead eggs and larvae in late February ($\hat{M}_r$)		Estimated fractions of eggs and larvae dying—		
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Early	Shortly before hatching	After hatching
Harris River	0.27	±0.06	0.50	±0.14	0.27	0.14	0.09
Indian Creek	.10	±.04	.75	±.10	.10	.54	.11
Twelvemile Creek	.27	±.06	.41	±.10	.27	.12	.02

[1] All samples were collected from intertidal riffles.

1957. Since spawning density was not estimated in 1956, no estimates of M_t are given. Also, because of small sample size, it is not possible to give meaningful estimates of p_0. Thus, for the 1956 brood year, only estimates of M_r are given to indicate time and magnitude of mortality (table 5).

In autumn 1956, egg mortality appeared to be highest after embryos had eyed. The February sample included three general categories of dead specimens: (1) Embryos dying early (as evidenced by the opacity and advanced decomposition of the eggs), (2) embryos dying just before hatching (as evidenced by development of body structures), and (3) larvae dying after hatching. Table 5 gives estimates of the fractions of total deaths occurring early, shortly before hatching, and after hatching.

Two features of these data stand out. First, early egg mortality was lowest in intertidal Indian Creek ($\hat{M}_r=0.10$ versus $\hat{M}_r=0.27$ in intertidal Harris River and Twelvemile Creek). Second, this relation had reversed by late February. Other evidence, which will be considered later, strongly suggests that freezing was the major cause of mortality of the 1956 brood shortly before and after hatching.

With regard to early egg mortality possibly associated with oxygen supply and related factors, evidence from 1956 brood year embryos does not contradict the possibility that intertidal Indian Creek provides a more suitable environment than either intertidal Harris River or Twelvemile Creek.

1957 Brood Year

Estimated mortality of the 1957 brood year provided the most striking evidence obtained in the course of these studies on relation between oxygen supply and egg mortality. As shown in figure 6, mean dissolved oxygen levels during the spawning period in 1957 were less than 50 percent of other years. These low levels of dissolved oxygen occurred during a prolonged period of low precipitation and discharge. For example, between August 10 and September 25, discharge of Indian Creek exceeded 20 c.f.s. only 30 percent of the time. Also, over this period very low discharge (4 to 10 c.f.s.) prevailed for 2 weeks during and after spawning. Furthermore, clear skies prevailing over the latter half of September were thought to have contributed to an unusually prolific growth of periphyton observed on the surface of streambeds at the time.

The escapement of adults was the lowest observed during these studies. The density of adult female pink and chum salmon spawning in intertidal areas of the study streams was five or less per 100 m.². The period of spawning lasted only from about September 7–17, the briefest period observed.

There was good evidence that egg mortality was high after spawning in 1957. Eggs were collected from riffles B and C in intertidal Indian Creek and riffles E and F in intertidal Twelvemile Creek during early November 1957 and late March 1958 and from intertidal Harris River in early April 1958.

Because differences in estimated values of M_r were not significant among the study riffles sampled, samples collected from intertidal Indian and Twelvemile Creeks were pooled by date to give the following single estimates of M_r and their 90-percent confidence limits:

$$\text{November} \quad \hat{M}_r=0.69\pm0.19$$

$$\text{March} \quad \hat{M}_r=0.57\pm0.24$$

Difference between the two estimates is not significant. The data indicate that mortality was igh before hatching and low after hatching.

Most dead eggs collected in November already ad decayed considerably and were classified as ragments, suggesting that mortality occurred hortly after spawning. This finding would not e unexpected because dissolved oxygen levels ere unusually low during spawning. Further- ore, there was evidence of high biochemical xygen demand continuing well into autumn 1957. lthough oxygen levels had increased significantly etween August and November 1957, they were till lower in November 1957 than in August 1958, ven though water temperatures were about ° C. cooler in November 1957 than in August 958 (McNeil, 1962b).

The high percentage of fragments among dead pecimens collected from intertidal Indian and welvemile Creeks in November 1957 remained irtually unchanged through March 1958. The alues were:

INDIAN CREEK

Riffle B: 92 percent in November and 96 percent in March.
Riffle C: 70 percent in November and 70 percent in March.

TWELVEMILE CREEK

Riffle E: 66 percent in November and 76 percent in March.
Riffle F: 97 percent in November and 95 percent in March.

his was nearly conclusive evidence that estimates M_r obtained from egg fragments alone would little changed over late autumn and winter, nd estimates of M_r based on presence of egg agments and made in early spring 1958 would ve essentially the same result as estimates made e previous autumn.

Intertidal Harris River was sampled about pril 1, 1958, when egg fragments or live larvae ere collected at 34 points. Only egg fragments ere found at 31 of the 34 points, giving minimal timates of

$$M_t \geq M_r = 31/34 = 0.91$$

The available evidence suggested that condi- ns in 1957 were unfavorable for egg survival, d exceptionally high egg mortality occurred in study streams. This high mortality was associated with unusually low levels of dissolved oxygen in intragravel water and low density of spawners. Unexpectedly low levels of dissolved oxygen prevailed into November 1957, suggesting that the biochemical oxygen demand was unusually high. There is a possibility that the density of females spawning (five or less per 100 m.^{2}) was too low to remove accumulated organic detritus from spawning beds in quantities sufficient to reduce materially the biochemical oxygen demand (Ricker, 1962; McNeil and Ahnell, 1964).

1958 Brood Year

Adult escapements were moderately low in 1958, though considerably higher than in 1957. Spawning densities ranged from 13 females per 100 m.^{2} in intertidal Harris River and Indian Creek to 1 and 2 females per 100 m.^{2} in upstream Twelvemile Creek and Harris River, respectively. Density of spawning females in intertidal Twelvemile Creek was 11 per 100 m.^{2}

Hydrological conditions during spawning favored a higher egg survival than in 1957. Indian Creek maintained discharges of 10 c.f.s. or more over the spawning period as opposed to a minimum discharge of 4 c.f.s. during spawning in 1957, when high early egg mortality occurred.

Observations on mortality were made in intertidal Harris River, Indian Creek, and Twelvemile Creek. Spawning densities in upstream Harris River and Twelvemile Creek were too light to warrant investigations in these areas. Table 6 summarizes the results of the mortality estimates.

For purposes of the present discussions, intertidal Twelvemile Creek can be dismissed because of extreme high early mortality ($\hat{M}_t = 0.97$ by late November) apparently caused by scouring during floods, which physically removed eggs from the spawning bed.[6] As a consequence, there were insufficient numbers of eggs remaining to relate observations on mortality to observations on factors affecting oxygen supply. Workers resampled the area in December primarily to check the results of the November sampling.

The numbers of eggs collected approached expectation in intertidal Harris River and Indian Creek. Indian Creek was sampled on one

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[6] Potential egg deposition in intertidal Twelvemile Creek during September 1958 was estimated to be 175 per m.^{2} By late November, mean density of live plus dead eggs was estimated to be only four per m.^{2}; by late December only one per m.^{2}

TABLE 6.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1958 brood-year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Sept. 18	0.26	[1] ±0.25	0.01	±0.01	1.00	----------
Nov. 15	.51	[1] ±.35	.16	±.23	.96	±0.06
Dec. 20	.84	±.21	.66	±.38	.82	±.12
Intertidal Indian Greek:						
Nov. 15	0	[1] ±.39	.13	±.13	.90	±.07
Intertidal Twelve mile Creek:						
Nov. 30	.97	±.04	----------	----------	1.00	----------
Dec. 28	.99	±.01	----------	----------	1.00	----------

[1] These estimates of M_t were obtained with log-transformed data.

occasion only (mid-November), and comparisons between the two areas will be limited to the mid-November samples.

The expected number of eggs based on potential deposition was 201 per m.^{2} in both intertidal Harris River and Indian Creek. In mid-November the difference between mean estimates of M_r ($\hat{M}_r=0.16$ in intertidal Harris River, and $\hat{M}_r=0.13$ in intertidal Indian Creek) was not statistically significant. Furthermore, a comparison of values of $\hat{p}_0$ in November gave a chi-square value of 0.46 (1 d.f.), indicating no significant difference in the frequency of occurrence of dead eggs in intertidal Harris River and Indian Creek. Hence, for the 1958 brood year, there was no conclusive evidence of higher egg mortality in intertidal Harris River than in intertidal Indian Creek. It is noteworthy, perhaps, that in intertidal Harris River $\hat{M}_r$ increased significantly between mid-November and mid-December. It is not known if a similar increase occurred in intertidal Indian Creek.

1959 Brood Year

Density of spawners was highly variable among and within the study streams in 1959. Estimated densities of females spawning were:

Intertidal Harris River	25 females per 100 m.^{2}
Upstream Harris River	6 females per 100 m.^{2}
Intertidal Indian Creek	46 females per 100 m.^{2}
Intertidal Twelvemile Creek	15 females per 100 m.^{2}
Upstream Twelvemile Creek	1 female per 100 m.^{2}

Because of the very low density of spawning adults, mortality was not studied in upstream Twelvemile Creek, but observations on mortality were made in upstream Harris River. High stream discharge occurred during spawning, providing more favorable conditions for egg survival during spawning than in 1957. Results of studies on mortality of the 1959 brood year are summarized in table 7.

As observed in 1958, mortality in intertidal Twelvemile Creek was very high initially and apparently was associated again with the direct removal of eggs from the spawning bed. Since estimates from upstream Harris River indicated

TABLE 7.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1959 brood year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$ [1]	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Oct. 6	0.27	±0.24	0.08	±0.06	0.97	±0.03
Oct. 20	.35	[2] ±.21	.11	±.09	.89	±.07
Upstream Harris River:						
Nov. 4	.73	±.23	.17	±.33	.99	±.01
Intertidal Indian Creek:						
Oct. 10	.52	±.18	.08	±.07	.96	±.04
Nov. 10	.27	±.29	.02	±.01	.90	±.08
Intertidal Twelve-mile Creek:						
Oct. 27	.95	±.07	----------	----------	1.00	----------

[1] p_0 is the fraction of points containing fewer than 35 dead eggs per square meter.
[2] This estimate of M_t was obtained from log-transformed data.

nuch the same thing, these areas proved to be of ittle value in evaluating relations between nortality and oxygen supply.

Differences in mortality level between intertidal Harris River and Indian Creek could not be emonstrated with estimates of M_r and M_t. However, estimates of p_0 made in mid-October howed that samples containing 35 or more dead ggs per m.^{2} occurred with almost equal frequency n intertidal Harris River and Indian Creek espite much lower spawning density in intertidal Harris River (about 53 percent of intertidal ndian Creek). This evidence suggested that egg nortality was higher in intertidal Harris River han in intertidal Indian Creek.

960 Brood Year

Egg mortality was studied in intertidal Twelvemile Creek, Harris River, and Indian Creek table 8).

High early mortality from causes associated vith the direct removal of affected specimens from he spawning bed occurred in intertidal Twelvemile Creek for the third year. In 1960, however, nost of this high mortality occurred during spawning ($\hat{M}_t$=0.71 in late September).[7] Since mortality from causes associated with spawning (e.g., edd superimposition) is beyond the scope of this aper, these causes will not be considered further ere. By late November there was evidence of ncreased egg mortality in intertidal Twelvemile Creek, but this mortality was relatively low.

The density of females spawning in intertidal Harris River and Indian Creek was relatively high nd nearly equal. Late in September at the conclusion of spawning, estimates of M_r and p_0 were very nearly the same for these two areas. At hatching, however, 35 or more dead eggs per m.^{2} were found at 26 percent of the points sampled in intertidal Harris River and at only 10 percent of the points sampled in intertidal Indian Creek. Estimates of $\hat{M}_r$ also indicated that mortality of eggs remaining in the streambed was higher in intertidal Harris River than in intertidal Indian Creek.

STABILITY OF THE SPAWNING BED AND MORTALITY

Two factors causing gravel to shift in spawning beds are flooding and females digging redds. The importance of redd superimposition as a factor limiting production of salmon fry is beyond the scope of this paper and will not be considered. My discussions will be limited to the influence of flooding and debris movement on egg and larval mortality.

Mortality caused by gravel shift would make itself evident by complete disappearance of eggs and larvae from spawning beds. Changes in abundance and distribution of eggs and larvae will be examined to obtain evidence of mortality caused by gravel movement. Three population parameters will be considered in evaluating the stability of spawning beds: (1) Total mortality (M_t), (2) mean abundance of eggs and larvae per m.^{2} (live plus dead)($\bar{P}$), (3) fraction of points containing fewer than 35 live plus dead eggs per m.^{2} (p_0').

High discharge occurs most frequently in Southeastern Alaska streams during October, November, and December. Autumn storms are often accompanied by heavy rain which sometimes

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[7] This same phenomenon was also observed in 1961 (unpublished data, RI, University of Washington, Seattle).

TABLE 8.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1960 brood year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$ [1]	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
tertidal Harris River:						
ept. 28	0.29	±0.18	0.03	±0.01	0.92	±0.05
Dec. 2	.69	±.09	.18	±.07	.74	±.07
te tidal Indian Creek:						
Sept. 22	.44	±.20	.05	±.05	.91	±.05
Nov. 22	.50	±.22	.12	±.08	.90	±.06
tertidal Twelve-mile Creek:						
Sept. 30	.71	±.17	.02	±.03	.98	±.02
Nov. 30	.75	[2] ±.08	.11	±.11	.92	±.03

[1] p_0 is the fraction of points containing less than 35 dead eggs per square meter.
[2] This estimate of M_t was obtained with log-transformed data.

Table 9.—*Dates on which rain[1] at Hollis, Alaska, exceeded 4.0 inches in 72 hours, 1956–60*

Dates precipitation exceeded 4.0 inches in a 72-hour period	Amount
	Inches
1956	
None	
1957	
Nov. 21–23	4.08
1958	
Oct. 19–21	6.79
Oct. 28–31	5.08
Nov. 7–9	4.14
1959	
Nov. 5–7	5.32
Dec. 5–7	7.02
1960	
Oct. 9–11	4.31
Oct. 20–22	4.08

[1] Data provided by Northern Forest Experiment Station, U.S. Forest Service, Juneau, Alaska.

continues over several days. To index periods of heavy precipitation, dates on which total precipitation exceeded 4 inches in 72 hours at Hollis (fig. 4) are given in table 9. Stream discharge records revealed that unusually high discharges accompanied rainfall of this high intensity. The analysis showed that rain was most intense in 1958 and 1959 and least intense in 1956 and 1957.

Although a comprehensive evaluation of mortality of 1956 and 1957 brood year eggs and larvae was not feasible because of limited sampling, estimates of M_r obtained for these brood years (and discussed previously) gave no indication of losses occurring from spawning beds. Observations on subsequent brood years (1958 and 1959 particularly) have shown, however, that gravel movement during high discharge is an important cause of mortality in the study streams.

1958 Brood Year

Rainfall exceeded 4.0 inches in 72 hours three times between October 19 and November 9, 1958 (table 9). Samples of eggs were collected before and after the storms in intertidal Harris River and after the storms in intertidal Indian and Twelvemile Creeks (table 10).

The number of eggs ($\bar{P}$) estimated to be present in intertidal Harris River near the end of spawning agreed with the expected number (E') obtained from the estimated density of females spawning ($\hat{\bar{P}}=189$ and $E'=201$ per m.^{2}). After the three periods of heavy rainfall, the abundance of eggs had decreased significantly, and the fraction of points containing fewer than 35 eggs per m.^{2} had increased significantly ($X^2=5.5$, 1 d.f.). This was good evidence that a significant mortality attributable to gravel movement had occurred.

In Indian Creek, the number of eggs estimated to be present in November after the storms agreed with the expected number ($\hat{\bar{P}}=222$ and $E'=202$ eggs per m.^{2}); hence, there was no evidence of mortality from gravel movement in intertidal Indian Creek.

The number of eggs estimated in intertidal Twelvemile Creek after heavy rainfall was con-

Table 10.—*Estimates of the population parameters* E′, $\bar{P}$, p′$_0$, *and* M$_t$ *used to evaluate mortality of 1958 brood year eggs possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per m.^{2} (E' and $\hat{\bar{P}}$)		Fraction of points containing fewer than 35 eggs per m.^{2} ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:							
September 18 to	3	[1] 189	[2] ±101	0.71	±0.11	0.26	[2] ±0.25
November 15		[1] 104	[2] ±74	.83	±.09	.51	[2] ±.35
Intertidal Indian Creek							
September 20 to	3	[3] 201					
November 15		[1] 223	[2] ±84				
Intertidal Twelvemile Creek:							
September 25 to	3	[3] 174					
November 30		4	±6				

[1] Estimated number of live plus dead specimens in the spawning bed ($\hat{\bar{P}}$).
[2] These limits were set with log-transformed data.
[3] Expected number of specimens based on potential egg deposition (E').

siderably less than the expected number. It was thought initially that high discharge caused mortality; however, samples were not collected before heavy precipitation in 1958, and it will be shown subsequently that high mortality of 1960 brood year eggs in Twelvemile Creek occurred in association with spawning before the storms.

1959 Brood Year

Heavy rainfall occurred in early November and December 1959. The evidence indicated that mortality occurred in association with heavy rain in all areas sampled (table 11).

The intertidal Harris River sampling program was modified slightly in 1959 to evaluate egg and larval losses associated with heavy precipitation. Because a sample taken November 16 did not include the entire area sampled on other dates, comparisons were limited to collections made within the area sampled on November 16. It is for this reason that estimates of M_t given in table 11 differ slightly from the estimates given in table 7 for the same dates. The area sampled on November 16 included 75 percent of the intertidal Harris River spawning area described in table 1.

Trees felled by loggers into upstream Harris River and transported through intertidal Harris River on the crests of two mid-October freshets appeared to cause little or no mortality. Nineteen spruce and hemlock trees, some more than 3 feet in diameter at the base of the trunk and more than 100 feet long, and several large alder trees were known to have floated through the intertidal zone. Estimates of $\hat{P}$, p'_0, and $\hat{M}_t$ were nearly the same for samples collected before (October 6) and after (October 20) the presence of floating trees.

There was evidence that mortality occurring in intertidal Harris River between October 20 and November 16 was caused by gravel movements during heavy rain. The total population of eggs was estimated to decline about 50 percent between these dates. Associated with this decline were increases in $\hat{p}'_0$ and $\hat{M}_t$.. The period of heavy rain

TABLE 11.—*Estimates of the population parameters* E', $\bar{P}$, p'_0, *and* M_t *used to evaluate mortality of 1959 brood year eggs and larvae possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per square meter (E' and $\hat{P}$)		Fraction of points containing fewer than 35 eggs per square meter ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River: [1]							
September 26		[2] 393					
to	None						
October 6		[3] 288	±105	0.59	±0.09	0.30	±0.26
to	None						
October 20		[3] 323	±138	.58	±.12	.28	±.33
to	1						
November 16		[3] 159	[4] ±77	.65	±.18	.64	[4] ±.20
to	1						
February 26		[3] 169	[4] ±46	.65	±.09	.73	[4] ±.08
Upstream Harris River:							
September 26		[2] 106					
to	None						
November 4		[3] 31	±26	.93	±.05	.73	±.23
to	2						
March 3		[3] 0				1.00	
Intertidal Indian Creek:							
September 26		[2] 705					
to	None						
October 10		[3] 346	±130	.59	±.09	.52	±.18
to	1						
November 10		[3] 530	±206	.51	±.13	.27	±.29
to	1						
February 29		[3] 24	±18	.91	±.06	.97	±.03
Intertidal Twelvemile Creek:							
October 1		[2] 229					
to	None						
October 27		[3] 11	±17	.99	±.06	.95	±.07
to	2						
February 21		[3] 1	±1	1.00		.99	±.002

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[1] Includes 75 percent of the area described in table 1.
[2] Expected number of specimens based on potential egg deposition (E').
[3] Estimated number of live plus dead specimens in the spawning bed ($\hat{P}$).
[4] These limits were set with log-transformed data.

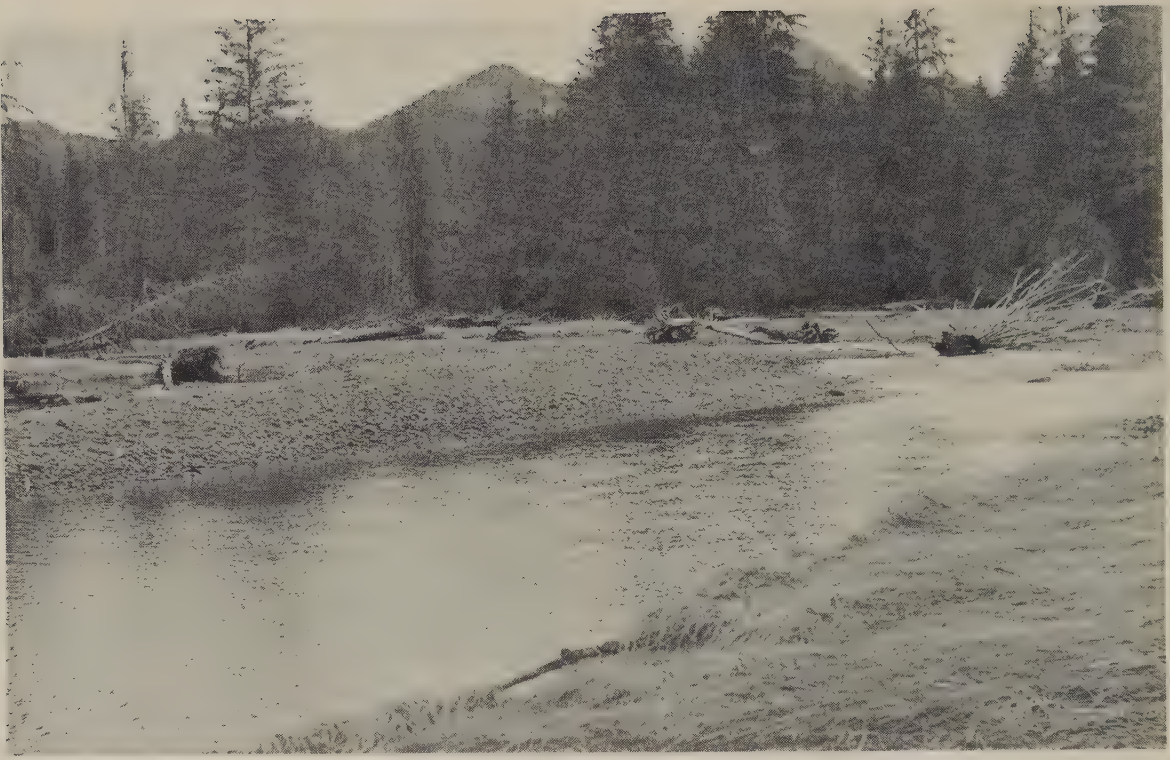

FIGURE 9.—Debris deposited in intertidal Indian Creek by the December 1959 flood.

in early December appeared to result in little additional loss of eggs or larvae from intertidal Harris River.

The period of heavy rain in November was not associated with high egg mortality in intertidal Indian Creek, but the period of heavy rain in December was associated with high mortality of eggs and larvae. After high water had receded in December, large numbers of eggs and larvae scoured from the Indian Creek streambed were observed by workers along the banks. About 90 percent of live eggs and larvae in the intertidal Indian Creek spawning bed at the time of high water in December 1959 were probably destroyed. A factor contributing to this high mortality appeared to be the breaking up of a natural log jam located a short distance above the intertidal Indian Creek spawning area and the subsequent deposition of debris from this jam in the spawning area. Figure 9 shows some of the debris deposited in intertidal Indian Creek. Turbulence created by the stream flowing around this debris was believed to have been mainly responsible for causing the stream to alter its course at several locations, washing out or burying deeply a large percentage of eggs and larvae present.

There was evidence that gravel movement caused high mortality in upstream Harris River. No live or dead eggs or larvae were collected from 68 points sampled in February 1960. Other evidence of widespread gravel movement in upstream Harris River was obtained from studies on size composition of bottom materials. There was a significant reduction in volumes of fine sands and silts in bottom materials during high water in autumn 1959 (McNeil and Ahnell, 1964).

1960 Brood Year

Periods of highest intensity rainfall occurred between October 9 and 22. Intertidal Harris River, Indian Creek, and Twelvemile Creek were sampled in autumn 1960 before and after high water (table 12).

Estimated total abundance of eggs in intertidal Harris River, as in the previous 2 years, declined about 50 percent in association with high water. The mean fraction of points containing fewer than 35 eggs per m.^{2} increased 0.16 after

TABLE 12.—*Estimates of the population parameters* E', $\overline{P}$, p'_0, *and* M_t *used to evaluate mortality of 1960 brood year eggs and larvae possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per m.² (E' and $\hat{\overline{P}}$)		Fraction of points containing fewer than 35 eggs per m.² ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:							
September 22		[1] 735					
to	None						
September 28		[2] 538	±132	0.33	±0.08	0.29	±0.18
to	2						
December 2		258	±72	.49	±.08	.69	±.09
Intertidal Indian Creek:							
September 21		[1] 708					
to	None						
September 22		[2] 436	±146	.52	±.09	.44	±.20
to	2						
November 22		[2] 380	±162	.47	±.11	.50	±.20
Intertidal Twelvemile Creek:							
September 28		[1] 381					
to	None						
September 30		114	±66	.68	±.11	.71	±.17
to	2						
November 30		103	[3] ±31	.68	±.11	.75	[3] ±.08

[1] Expected number of specimens based on potential egg deposition (E').

[2] Estimated live plus dead specimens in the spawning bed ($\hat{\overline{P}}$).

[3] These limits were set with log-transformed data.

heavy precipitation in 1960; while in 1958 and 1959 the increase was about 0.10. The difference between an increase of 0.16 and 0.10, however, was not statistically significant in these instances.

As in 1958 and 1959, on occasions when there was no movement of temporarily stationary debris with high water, eggs and larvae in intertidal Indian Creek apparently suffered little mortality. There was also no evidence of mortality associated with flooding in Twelvemile Creek in 1960, although large numbers of eggs had apparently disappeared before high water.

FREEZING OF INTRAGRAVEL WATER AND MORTALITY

The study streams freeze usually in December, January, and February. Hence, mortality attributable to freezing must occur either during or after hatching.

Maximum daytime air temperatures were used as as index of severity of freezing. Periods when daytime temperatures remained below freezing for two or more consecutive days were determined from air temperature records obtained at Hollis by the Northern Forest Experiment Station (table 13). Freezing was most severe in winters 1956–57 (1956 brood year) and 1958–59 (1958 brood year).

1956 Brood Year

There was evidence of high mortality from freezing in winter 1956–57. Estimates of M_r for the 1956 brood year in each of the study streams are summarized in table 5. Mean values of M_r were found to increase between late November 1956 and late February 1957 as follows:

$\hat{M}_r=0.27$ to $\hat{M}_r=0.50$ in intertidal Harris River.

$\hat{M}_r=0.10$ to $\hat{M}_r=0.75$ in intertidal Indian Creek.

$\hat{M}_r=0.27$ to $\hat{M}_r=0.41$ in intertidal Twelvemile Creek.

TABLE 13.—*Periods of daytime freezing and associated precipitation at Hollis, Alaska 1956–61* [1]

Dates when maximum temperature was less than 0° C.	Mean temperature at 5 p.m.	Precipitation
	°C.	*Inches*
Winter 1956–57:		
Dec. 3–12	−4°	[2] 2.03
Jan. 7–13	−6°	0
Jan. 20–26	−7°	0
Feb. 22–25	−6°	0
Winter 1957–58:		
None		
Winter 1958–59:		
Jan. 1–8	−5°	0
Winter 1959–60:		
None		
Winter 1960–61:		
None		

[1] Data provided by Northern Forest Experiment Station, U.S. Forest Service, Juneau, Alaska.

[2] Fell as snow, given as inches of rain.

Two classes of dead eggs and larvae not present in November samples were found in February samples: dead eggs with well-developed embryos ready to hatch and dead larvae. Death of eggs containing the well-developed embryos occurred after November sampling and before hatching in December.

This prehatching mortality occurred in conjunction with the December 3 to 12 freezeup. The observed posthatching mortality may have been caused, for the most part, by the subsequent more severe periods of freezing in January and February.

I have already summarized in table 5 the estimated fractions of 1956 brood year eggs and larvae dying early, shortly before hatching, and after hatching. Assuming that mortality at and after hatching was caused by freezing, I estimated mortality of the 1956 brood year from freezing to be about 23 percent in Harris River riffle A, 65 percent in Indian Creek riffles B and C, and 14 percent in Twelvemile Creek riffles D and E.

I visited the study streams during the February 22–25 freeze. Except for an occasional exposed riffle, they were coated with ice several inches thick. Freezing appeared to have a greater effect on Indian Creek spawning beds than on Harris River and Twelvemile Creek spawning beds. I attempted to drive metal rods into the Indian Creek streambed at a number of locations. The gravel was often frozen, particularly where exposed by drying of the stream. Anchor ice also had formed at several points examined.

One important conclusion to be drawn from these data is that mortality associated with freezing was highest in the stream having the lowest minimum discharge (4 c.f.s. in Indian Creek as compared with 12 c.f.s. in Twelvemile Creek and 22 c.f.s. in Harris River).

1958 Brood Year

Freezing occurred after hatching in January 1959. Sampling was undertaken in March 1959 (2½ months after freezing), and the possibility that larvae killed by freezing had decayed before sampling could not be ignored. Therefore, the best evidence of winter mortality possibly associated with freezing may be estimates of M_t which are summarized in table 14.

In intertidal Harris River, mortality was high before freezing and there was no evidence of additional mortality over winter. Intertidal Indian Creek, on the other hand, experienced high mortality over winter, thus supporting earlier findings with 1956 brood year eggs and larvae. There was no evidence of winter mortality in intertidal Twelvemile Creek, but because of the scarcity of larvae in the spawning bed, it is highly unlikely that mortality would have been detected here.

TABLE 14.—*Estimated total mortality of 1958 brood year pink and chum salmon eggs and larvae before and after freezing in winter 1958–59*

Spawning area and date	$\hat{M}_t$	
	Mean	90-percent confidence limits of the mean
Intertidal Harris River:		
Dec. 20, 1958	0.84	±0.21
Apr. 5, 1959	.62	±.29
Intertidal Indian Creek:		
Nov. 15, 1958	0	[1] ±.39
March 28, 1959	.64	±.28
Intertidal Twelvemile Creek:		
Dec. 28, 1958	.99	±.01
March 24, 1959	.99	±.01

[1] This limit was set with log-transformed data.

Other Brood Years

According to Hollis air temperatures, there were no prolonged periods of freezing that would affect eggs and larvae of the 1957, 1959, and 1960 brood years. An examination of data on mortality revealed little evidence of mortality possibly caused by freezing.

There was no evidence of winter mortality of the 1957 brood year. Prewinter and postwinter pooled estimates of M_r for riffles B, C, E, and F and their 90-percent confidence limits were:

$$\hat{M}_r \text{ (pooled for November)} = 0.69 \pm 0.19$$

$$\hat{M}_r \text{ (pooled for March)} = 0.57 \pm 0.24$$

With regard to the 1959 brood year, there was a rather high incidence (18 percent) of dead larvae in samples collected from intertidal Harris River on February 26, 1960, but a low incidence (less than 1 percent) of dead larvae collected in samples from intertidal Indian Creek. Factors other than freezing probably were responsible for the mortality observed in intertidal Harris River because temperatures were mostly above freezing in winter 1959–60, and few dead larvae were found in intertidal Indian Creek. Scarcity of eggs and larvae in

Twelvemile Creek spawning areas made it impractical to evaluate winter mortality there.

Only a small number (about 1 percent) of 1960 brood year larvae collected in late winter 1961 from intertidal Harris River and Indian Creek were dead. Of 933 larvae collected in intertidal Twelvemile Creek, 9.4 percent were dead, but most dead larvae were found in one redd. Factors other than freezing were suspected of having caused their death.

An experiment indicated that little or no freezing of intragravel water occurred in winter 1960–61. One-half-dram vials were filled with water and buried 5 and 10 inches in spawning beds during autumn 1960. They were recovered in spring 1961 and examined for breakage caused by water expanding during freezing. The recovery of a broken vial was used to indicate occurrence of freezing at the point of burial. Breakage from causes other than freezing was minimized by enclosing vials in latex tubing. Sixty-three vials were recovered from intertidal Indian Creek, 36 from intertidal Harris River, and 30 from intertidal Twelvemile Creek. There were no broken vials in the lot. This experiment provided further evidence that intragravel water did not freeze in winter 1960–61.

DISCUSSION AND CONCLUSIONS

There is evidence that mortality of pink and chum salmon from egg deposition to fry migration is seldom less than 75 percent and commonly exceeds 90 percent in small coastal streams. Freshwater mortality, therefore, may place more severe restrictions on production of pink and chum salmon than natural salt-water mortality.

A thorough understanding of the ecological and physiological requirements of pink and chum salmon eggs and larvae is necessary for evaluating the potential of spawning beds to produce fry. It has been a goal of these studies to determine the relative importance of certain factors affecting quality of the spawning bed environment and fry production.

OXYGEN SUPPLY AND RELATED FACTORS

It is evident from a review of the literature that the oxygen supply rate to an egg or larva is a function of oxygen content and velocity of flow of intragravel water, both of which are affected by a complex of interacting factors. It would appear that oxygen privation is more critical in embryonic than in larval stages. For evaluating mortality possibly resulting from an oxygen deficiency, observations on mortality were based primarily on the population of eggs present in the spawning bed at the time of sampling. Where large numbers of eggs had disappeared from spawning beds before sampling, or where density of females spawning was light, it was not possible with the sampling scheme used to obtain data adequate to evaluate prehatching mortality possibly associated with the availability of oxygen. Inadequate data for the intertidal Twelvemile Creek and upstream Harris River and Twelvemile Creek spawning areas were of limited value in evaluating mortality possibly due to oxygen privation, and observations were made mostly in intertidal Harris River and Indian Creek.

Data on (1) dissolved oxygen content of intragravel water, (2) streambed gradient, and (3) organic content, size composition, and permeability of bottom materials showed more favorable oxygen supply in intertidal Indian Creek than in intertidal Harris River. Furthermore, results of mortality studies suggested that prehatching mortality not associated with the disappearance of eggs was lower in intertidal Indian Creek than in intertidal Harris River. Hence, there was general agreement between observations on physical quality of the spawning bed environment and egg mortality.

An opportunity arose in 1957 to evaluate the relation between prolonged low streamflow during spawning and egg mortality. In this instance, unusually low levels of dissolved oxygen in intragravel water were observed during the spawning period. The evidence relating an exceptionally high egg mortality to low streamflow corroborated the findings of other workers (Brett, 1951; Neave and Wickett, 1953; Wickett, 1958).

In these studies it was not possible to demonstrate a direct dependence of egg mortality and population size. In 1957, when spawning densities were extremely low and egg mortality was unusually high, there appeared to be some justification for suggesting that a minimum number of spawners is required to reduce the overall biochemical oxygen demand through the removal of organic detritus from spawning beds (Ricker, 1962). Additional research will be required to resolve this question.

STABILITY OF THE SPAWNING BED

Instability of the spawning bed was an important cause of egg and larval mortality in the study streams. There was no apparent relation between gravel composition and stability during flooding, and high mortality occurred in spawning beds composed of coarse and fine materials. Change in position of temporarily stationary debris caused gravel movement, but the presence of floating debris had little or no effect on gravel movement.

The influence of temporarily stationary debris on the stability of bottom materials was studied in Maybeso Creek (fig. 4), a stream located near Hollis (Bishop and Shapley, 1963). The results of this study gave further support to relations observed between movement of wood debris and mortality of eggs and larvae in Harris River, Indian Creek, and Twelvemile Creek.

High discharge may be a common cause of mortality among salmonid eggs and larvae. In New Zealand, Hobbs (1937) concluded that floods seldom destroyed salmon and trout redds, but at times accounted for a partial failure of a brood year. At Sagehen Creek, Calif., a flood in December 1955 destroyed brook trout, *Salvelinus fontinalis*, and brown trout eggs, causing the complete failure of the zero age group of these species in 1956 (Needham and Jones, 1959).

Observations on dislodgment of salmon eggs and larvae from British Columbia and Southeastern Alaska streams during flooding also have been reported. After flooding, Withler (1952) found preemergent sockeye salmon fry washed from a tributary of Babine Lake, British Columbia, and Wickett (1959) reported the observation of coho and chum salmon eggs on banks and in bushes along the Qualicum River, Vancouver Island. Floods at Sashin Creek in 1941 and 1943 were thought to have killed many pink salmon eggs and larvae (Hutchinson and Shuman, 1942; Davidson and Hutchinson, 1943).

FREEZING OF INTRAGRAVEL WATER

Although freezing has been considered an important cause of mortality, except for Neave (1947), Smirnov (1947), and Semko (1954), little direct evidence showing freezing to be an important cause of pink and chum salmon egg and larval mortality has been reported. I found that freezing caused high mortality of 1956 brood year eggs and larvae, particularly in intertidal Indian Creek. There was also an indication that the 1958 brood year experienced similar high mortality in Indian Creek. Winters of 1957–58, 1959–60, and 1960–61 were mild by comparison, and there was little or no evidence of mortality from freezing.

It was apparent that freezing exerted the greatest influence on mortality in the stream having the lowest minimum discharge. Further study may reveal that certain spawning areas are unproductive because of low discharge during periods of freezing. There was no evidence of high mortality from freezing during winters that maximum daytime air temperatures remained above 0° C.

SUMMARY

1. The available evidence indicates that high mortality of eggs and larvae greatly limits the abundance of juvenile pink and chum salmon. Proper management of pink and chum salmon fisheries will depend in part on a thorough understanding of the factors affecting the potential of spawning beds to produce fry. Field studies of egg and larval mortality are important because they provide information on time and magnitude of mortality that can be associated with causative factors.

2. In the study streams, egg mortality after the end of spawning seldom exceeded 20 percent in the absence of low levels of dissolved oxygen, freezing, or high water. There was evidence that mortality attributable to oxygen privation was highest where water circulation within the spawning bed was impaired.

3. Low levels of dissolved oxygen in intragravel water as well as high egg mortality occurred with low flow during and shortly after spawning. The resulting mortality of eggs was estimated to vary between 60 and 90 percent in the spawning areas sampled.

4. Movement of bottom materials during high water was an important cause of mortality, which was most severe where temporarily stationary debris shifted position within the flood plain. Mortality from movement of bottom materials was estimated to exceed 90 percent in one instance.

5. Freezing was an important cause of mortality only when maximum daytime temperatures remained below 0° C. for at least 2 consecutive days. Mortality from freezing was highest in the stream having the lowest minimum discharge, and was estimated to approach 65 percent on one occasion.

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CORRECTIONS FOR RECENT ISSUES OF THE FISHERY BULLETIN

VOLUME 63, NO. 3

Page 561, table 11. In the head of second column the M should have a subscript 1, not superscript 1.

Page 562, left column, 6th line from bottom. In the first exponent of the equation for p, the M should have a subscript (M_1).

Page 569, right column, 6th line from bottom. The product quantity 2.894 (1.4577) should be 2.894 (.4577).

Page 659, left column, 2d paragraph. Both x's in equation should read $\bar{x}$.

Page 663, right column, 2d full paragraph, 9th line. The figure is 629,000.

Page 666, right column, last line. Equation should read: $(0.22)(0.04)+(0.78)P_A=0.48$ or $P_A=0.60$.

Page 667, left column, 3d paragraph, 10th line. Should read: to the model given earlier (page 661).

Page 669, right column, 4th and 5th lines should read: the Commander Islands recovery data (appendix table 2).

VOLUME 64:

Page 215, right column. The author Florkin, Marcel, should be moved up 4 lines to appear before the 1934a.

Page 220, figure 197. The scale should read 0 to 5.0.

Page 299, figure 268. Legend should read: Slightly slanted tangential section through the opening and adjacent portion of the ovary of *C. virginica.* Oviduct with two eggs at lower left side. Kidney reservoir at lower right. Ovary follicles at top. Drawn semidiagrammatically from a photomicrograph of a preparation. Kahle, hematoxylin-eosin.

Page 349, figure 329. The identification letters, a through f, should be added below the individual figures starting with upper row and reading from left to right.

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